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STUDIES ON THE ECOLOGY OF COFFEE PLANTATIONS IN EAST AFRICA. II.

THE AUTECOLOGY OF *ANTESTIA* SPP. (PENTATOMIDAE) WITH A PARTICULAR ACCOUNT OF A STREPSIPTEROUS PARASITE

By T. W. Kirkpatrick, M.A., F.R.E.S.

(*Entomologist, East African Agricultural Research Station, Amani, Tanganyika Territory.*)

[Read 5th May, 1937.]

With Forty Text-figures and Thirty-two Tables.

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INTRODUCTION.

SINCE the researches of Nassonov (1892–93) very little has been added to our knowledge of the biology of Strepsiptera. Moreover, Nassonov's work dealt with species parasitising Hymenoptera and, on account of the habits of their hosts, exact studies on such species are naturally attended with the greatest difficulty.

When therefore I found, early in 1935, a species of Strepsiptera parasitising the Pentatomid *Antestia*, the " Variegated Coffee Bug," which is one of the most serious and widespread pests of coffee in East Africa, the opportunity was taken to make a detailed study of its life-history. This is described in Parts II and III of this paper.

One clearly cannot study a parasite apart from its host, and during the course of my investigations several new facts about *Antestia* were discovered. It therefore seemed desirable to include in this paper a general account of *Antestia*, partly in order to render intelligible the detailed account of its Strepsipterous parasite, but even more because a collation and discussion of the information already gained is an essential preliminary to further work on this pest.

That further work is necessary will be obvious from Part I of this paper. It is especially desirable to obtain more knowledge of the influence of different environmental conditions on the feeding habits of *Antestia* and, in consequence, on the nature and extent of the damage caused.

Acknowledgements. I am indebted to Sir Guy A. K. Marshall and the specialists of the Imperial Institute of Entomology, for identifications of insects. Particularly to Dr. K. G. Blair for describing *Corioxenos antestiae*, and to Mr. W. E. China for identifying and giving other information about the species of *Antestia*. To the staff of the Coffee Experimental Station, Lyamungu, for assistance while I was working there and for sending me collections of *Antestia* when I was unable to go myself. To the entomological staff of the Department of Agriculture, Kenya, for collections of *Antestia* and various information acknowledged in the course of this paper. To Mr. L. R. Doughty, Geneticist of the East African Agricultural Research Station, for advice on the statistical treatment of certain problems, and to Mr. R. E. Moreau, Secretary, for reading over the typescript.

PART I.

THE BIONOMICS AND CONTROL OF *ANTESTIA*.

(1) The species of *Antestia* occurring on coffee in East Africa.

There is some difficulty in determining the distribution of the various species of *Antestia* in East Africa, since there has been much confusion in the nomenclature of this genus.

Anderson (1919), referring to the species common in Kenya, wrote : " Until recently, the bug was known as *Antestia variegata* Thunb. var. *lineaticollis* Stål, but Professor Schouteden has, after the examination of much material, come to the conclusion that they are quite distinct and has made *lineaticollis* a separate species. The East African coffee bug is, therefore, now known as *Antestia lineaticollis* Stål."

A. variegata Thunb. has been recorded from coffee in Nyasaland (Ballard, 1913) and in Southern Nigeria (Peacock, 1913), but I think it probable that both these records refer to another species, perhaps *lineaticollis*. The true *A. variegata* occurs in South Africa, where it is a pest of peaches (Lounsbury, 1918).

Gowdey (1918) referred to *A. orbitalis* Westw. var. *faceta* Germ. and *A. orbitalis* var. *lineaticollis* Stål, as occurring in Uganda and Kenya respectively. These two names have been adopted by many authors until recently, in spite of Schouteden's decision (Anderson, *loc. cit.*) and of the fact that ten years ago Hargreaves (1927) concluded that they were distinct species, since he was unable to interbreed them.

I recently sent specimens of five apparently distinct species of *Antestia* to the Imperial Institute of Entomology, and China (*in litt.*, 1936) has informed me that one of them is *A. trivialis* Stål, and, as regards the others, that he has "tentatively determined four 'species' as follows—*A. lineaticollis* Stål; *A. faceta* Germ.; *A. falsa* Schout.; *A. usambarica* Schout. Representatives of the last two have been sent to Dr. Schouteden for comparison with the types, and I am awaiting his reply."

I have myself no doubt that these are five distinct species and not varieties. I have attempted to interbreed them (except *usambarica* with any other and *falsa* with *trivialis*), but always without success. Moreover, as described in Part III, Section 9, they have different relationships with the Strepsipterous parasite *Corioxenos antestiae* Blair.

The colour pattern is variable, but I have not found any specimens definitely

Fig. 1.—*A. lineaticollis*. Pronotum and scutellum. × 10.

intermediate between any two of these species. Diagrams of typical colour patterns of the pronotum and mesothoracic scutellum are given in figs. 1–5. I believe, therefore, that the names and distribution of the East African species are as follows:—

A. lineaticollis Stål (fig. 1). Medium-sized, male about 6·8–7·5 mm., female 7·5–8·5 mm.* Predominant colours of dorsal surface black, orange, and white; rather shining and sharply contrasted owing to the sparse punctation in the light-coloured areas. The most widespread species. Dominant in most coffee districts of Kenya and Tanganyika, and in the Masaka, Mbarara, Mubende and Toro areas of Uganda (Hargreaves, 1930). Probably occurs in Nyasaland and Northern Rhodesia.

A. faceta Germ. (fig. 2). A small species, male 5·5–6·0 mm., female 6·5–7·0 mm. Colour of dorsal surface dark brown, orange tinged with magenta, and dirty white. The commonest species in the Masindi, Mengo, Buvuma Island and Bugishu districts of Uganda (Hargreaves, *loc. cit.*). Notley (1933) records it from the Nyanza province of Kenya, where it is apparently the dominant, if not the only species. In Tanganyika locally common on Kilimanjaro and in

* The measurements are the length from the apex of the head to the apex of the wings when folded. Exceptionally small or large specimens fall outside the limits given.

the South Paré mountains, but less so than *lineaticollis*. I have only found it in small numbers in the Usambara mountains. Recorded from Nyasaland (Smee, 1931).

2

Fig. 2.—*A. faceta*. Pronotum and scutellum × 10.

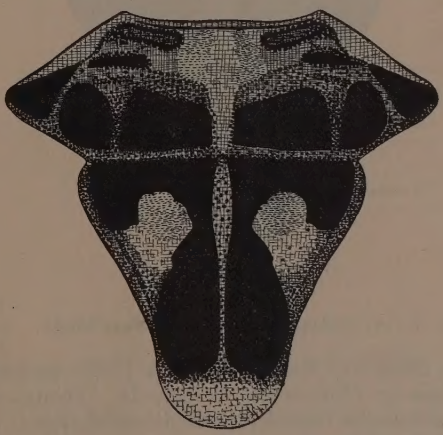

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Fig. 3.—*A. falsa*. Pronotum and scutellum. × 10.

A. falsa Schout. (fig. 3). Similar in colour to *faceta*, the orange parts rather more strongly tinged with magenta. Considerably larger, male about 8·3–8·8 mm., female 9·0–9·5 mm. I have found this species only in the South Paré mountains, where it was not common. I know of no other records from East Africa. I have been informed by Mr. J. M. Vrijdagh that it occurs in the Belgian Congo.

A. trivialis Stål (fig. 4). A large species, male 9·0–9·5 mm., female 10·0–10·7 mm. Predominant colour of dorsal surface olive brown; scutellum tinged with greenish-brown, its apex pale yellow; corium tinged purplish-brown.

Although the adult is so conspicuously distinct from any of the other species mentioned here, the immature stages are very similar, being mainly black, orange, and whitish. Not uncommon, though never abundant, in the East Usambara mountains. There are apparently no other records from East Africa.

A. usambarica Schout. (fig. 5). A large rather elongate species, male 9·5–10·0 mm., female 10·5–11·0 mm. The dark areas almost black, the pale markings yellow with at most a slight trace of orange, sometimes rather greenish-yellow. So far as is known, confined to the East and West Usambaras. I have only obtained a single specimen and have therefore been unable to make any experiments or observations on it. Both this species and *trivialis* were first taken by Morstatt (1912), though their names were not then determined. There are several specimens of both in the old German collection at Amani.

Fig. 4.—*A. trivialis*. Pronotum and scutellum. × 10.

In addition to these five species Hancock (1926) recorded *A. cincticollis* Shaum. on *Canthium* sp. (Rubiaceae) in Uganda. Though not yet found on coffee, it should perhaps be regarded as a potential pest.

Three other species of the genus have been recorded on coffee in other parts of the world. *A. clymeneis* Kirk. (vars. *galtiei* Frappa and *flaviventris* Frappa) is found in Madagascar (Frappa, 1933). This author states that this species feeds on both green and red coffee berries and in the laboratory also on fresh leaves. Injured berries usually turn black and drop.

A. partita Walk. (= *plebeia* Voll.) is said to be an important coffee pest in Java (Schumacher, 1919).

A. cruciata F. is recorded as attacking coffee in the Nilgiri hills in India (Fletcher, 1913).

(2) Life-history.

Much information has already been obtained by Anderson (1919) in Kenya, and by Gowdey (1918), Wilkinson (1924) and Hargreaves (1930, 1936) in

Uganda. It is therefore only necessary to give here a summary of the life-history, adding certain details not mentioned by these authors.

My own observations were made on bugs kept in the laboratory, each separately in a small celluloid cylinder, standing on blotting-paper and covered with a glass plate. They were fed on full-sized but still green coffee berries. The influence of other food on the duration of the life-cycle and on fecundity is discussed in Section 3.

The eggs are laid in batches, most often of 12, sometimes of 11 or 13. Anderson records several batches of 10 and one of 15. The last one, or two, batches laid before a female ceases ovipositing are often incomplete, consisting only of 4–6 eggs. Anderson also found that the first batch was occasionally incomplete.

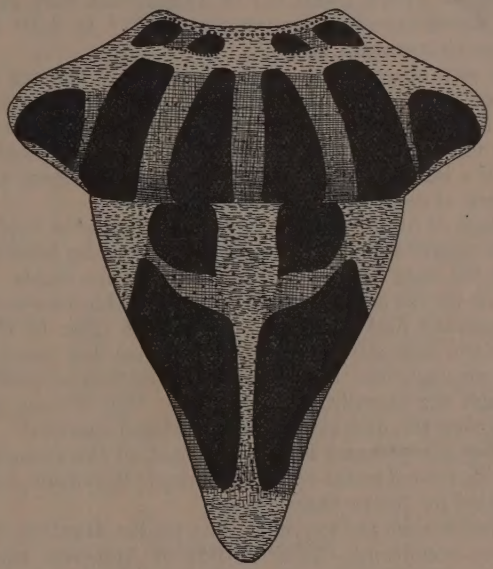

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Fig. 5.—*A. usambarica.* Pronotum and scutellum. × 10.

I have found that fertilised females, unless they are disturbed during the process, invariably lay their eggs in the manner precisely described by Wilkinson. Unfertilised females, however, often scatter their eggs at random.

The eggs are usually * laid on the under surface of a coffee leaf, sometimes on a berry or on other parts of the plant. Wilkinson records eggs on other plants growing near coffee, on tree trunks, and on the verandah of a house. It is improbable that nymphs hatching from eggs laid in such places would survive.

The number of eggs laid by a female is very variable. Anderson records one female that, during a period of 256 days, laid 41 batches totalling 485 eggs. The average he gives, for 61 bugs, is 126 eggs during a period of 89 days. My own records, at Amani, show an average of 13 batches laid by each fertilised

* According to Anderson, 90%.

female. This is slightly greater than Anderson's average; on the other hand, none of my females laid more than twenty batches. Hargreaves in Uganda has recorded over 300 eggs laid by one female.

I have found that unfertilised females lay only from one to four batches of eggs, though they may live for several months after ceasing to lay. Wilkinson records that females isolated after copulation never laid more than two batches. One of my females, however, laid four batches of fertile eggs during a period of 30 days after it had been segregated from a male.

The duration of the egg stage varies with the temperature. Anderson, at Kabete (6000 ft.) in Kenya, recorded 7–9 days during January to April and 13–15 days during May to December. Both Wilkinson and Hargreaves state that at Kampala (3900 ft.) in Uganda the period is between 4 and 9 days. My own records at Amani (3000 ft.) in Tanganyika vary from 5–6 days in February and March (average temperature 23·5°) * to 8–10 days in June to August (average temperature 19·2°).

Most of my own observations on the duration of the egg stage, as also, I believe, those of the other authorities quoted, were made under laboratory conditions. I have, however, several times compared the incubation period of eggs kept in the laboratory with that of eggs in the normal position on the under surface of a leaf of a coffee bush growing in the open, and I have never found a difference of more than a few hours.

The proportion of (unparasitised) eggs hatching in the field is, as stated by Wilkinson, very nearly 100%. I have found that under laboratory conditions, also, almost all the eggs laid by fertilised females are viable. All the eggs of one cluster hatch on the same day, and usually within two or three hours.

After eclosion the first-instar nymphs remain close to their empty egg-shells for about the first half of the stadium. Later they move away and begin to feed. They are, however, able to undergo the first ecdysis without having fed at all, though the mortality is then high. Only 12 out of 48 to which I gave no food during the first stadium moulted and survived.

With very few exceptions I have found that all the nymphs from one egg-batch moult to the second instar on the same day. Wilkinson, however, recorded several that varied by two or three days.

Tables 1–5 summarise the available data on the duration of the five stadia under laboratory conditions. (The records of Anderson and Wilkinson, as well as my own, show that there is no difference in the developmental period of the sexes.) Fig. 6, based on my records at Amani, shows how the period of development from egg to adult varies with the temperature.

A few experiments, made in an incubator, suggest that constant and rather high temperatures may have a retarding effect on development. However, only the duration of the fourth and fifth stadia was recorded, and the number of bugs in each experiment (seven) was perhaps insufficient. At an almost constant temperature of 30·0° the average duration of the fourth and fifth stadia together was 28·2 days; at 26·5°, 27·5 days; at 24·0°, 24·8 days; and at

* All temperatures in this paper are given in degrees centrigrade. The figures for average temperature were obtained from mercury-in-steel thermographs, checked frequently by an aspirated thermometer. They are $\frac{\text{max.} + \text{min.}}{2}$ after the application of a correction factor. The correction factor was obtained by summing the hourly temperatures on four or five days (chosen at random) in each month and dividing by 24. If the resulting average differed from the $\frac{\text{max.} + \text{min.}}{2}$ for the same days this correction was applied to the whole month. It was never greater than — 0·4°, and was frequently nil.

TABLE 1.

Antestia lineaticollis.

The duration of the first stadium.

Authority	Locality	Time of year	Average temperature	Mean duration (days)	Extremes
Gowdey	Kampala	Apr.	—	12	10–14
Wilkinson	Kampala	Sep.–Nov.	—	5·9	4–8
,,	,,	Nov.–Feb.	—	5·0	3–9
,,	,,	Feb.–Apr.	—	5·8	5–7
Anderson	Kabete	June–Aug.	—	15·1	10–18
,,	,,	Sep.–Feb.	—	9·2	6–10
Kirkpatrick	Amani	Dec.–Jan.	22·9–23·6	5·8	5½–6
,,	,,	May–June	20·8–21·7	8·0	7–9

TABLE 2.

Antestia lineaticollis.

The duration of the second stadium.

Authority	Locality	Time of year	Average temperature	Mean duration (days)	Extremes	Standard deviation	Standard error of mean
Gowdey	Kampala	Apr.–May	—	14	14–16	—	—
Wilkinson	Kampala	Sep.–Nov.	—	6	5–13	—	—
,,	,,	Nov.–Feb.	—	12·6	4–19	—	—
,,	,,	Feb.–Apr.	—	11·2	10–16	—	—
Anderson	Kabete	July–Sep.	—	33	11–47	—	—
,,	,,	Oct.–Feb.	—	20	18–28	—	—
Kirkpatrick	Amani	Jan.	23·1	9·4	9–11	0·58	0·13
,,	,,	May–June	21·3	13·6	11–22	4·55	0·57

TABLE 3.

Antestia lineaticollis.

The duration of the third stadium.

Authority	Locality	Time of year	Average temperature	Mean duration (days)	Extremes	Standard deviation	Standard error of mean
Gowdey	Kampala	May	—	15	13–16	—	—
Wilkinson	Kampala	Sep.–Nov.	—	10·5	7–16	—	—
,,	,,	Nov.–Feb.	—	11·3	6–23	—	—
,,	,,	Feb.–Apr.	—	8·0	5–11	—	—
Anderson	Kabete	Aug.–Oct.	—	22·5	8–66	—	—
,,	,,	Nov.–Mar.	—	15·8	13–27	—	—
Kirkpatrick	Amani	July (L), Aug. (L)	19·8–20·4	13·4	10–18	4·7	0·79
,,	,,	May (L), June (L) Apr. (V)	20·8–21·7	12·9	10–19	4·7	0·81
,,	,,	Apr. (L), Oct. (L) Nov. (V), Dec. (V)	21·9–22·6	12·4	10–20	3·3	0·61
,,	,,	Jan. (L), Feb. (L) Jan.–Mar. (V)	22·9–23·6	10·4	6–15	3·7	0·74

(L) = in laboratory; (V) = on enclosed verandah.

TABLE 4.

Antestia lineaticollis.

The duration of the fourth stadium.

Authority	Locality	Time of year	Average temperature	Mean duration (days)	Extremes	Standard deviation	Standard error of mean
Gowdey	Kampala	May–June	—	17	15–20	—	—
Wilkinson	Kampala	Sep.–Nov.	—	10·8	7–26	—	—
,,	,,	Nov.–Feb.	—	12·9	7–20	—	—
,,	,,	Feb.–Apr.	—	8·3	6–10	—	—
Anderson	Kabete	Sep.–Dec.	—	22·5	13–59	—	—
,,	,,	Dec.–Mar.	—	13·0	8–19	—	—
Kirkpatrick	Amani	June–Sep. (V)	18·9–19·5	17·6	10–27	6·75	0·75
,,	,,	July–Sep. (L) May (V)	19·8–20·4	14·8	10–24	8·6	0·98
,,	,,	May (L), June (L) Apr. (V), Oct. (V)	20·8–21·7	14·7	10–29	7·3	0·85
,,	,,	Apr. (L), Oct. (L) Nov. (L), Nov. (V) Dec. (V)	21·9–22·6	11·9	5–23	5·7	0·80
,,	,,	Dec.–Feb. (L) Jan.–Mar. (V)	22·9–23·6	10·5	7–17	4·55	0·43

(L) = in Laboratory; (V) = on enclosed verandah.

TABLE 5.

Antestia lineaticollis.

The duration of the fifth stadium.

Authority	Locality	Time of year	Average temperature	Mean duration (days)	Extremes	Standard deviation	Standard error of mean
Gowdey	Kampala	June–July	—	17	15–20	—	—
Wilkinson	Kampala	Sep.–Nov.	—	15·0	11–21	—	—
,,	,,	Nov.–Feb.	—	15·9	7–27	—	—
,,	,,	Feb.–Apr.	—	12·8	10–22	—	—
Anderson	Kabete	Sep.–Dec.	—	22·3	8–37	—	—
,,	,,	Dec.–Apr.	—	16·9	15–25	—	—
Kirkpatrick	Amani	June–Sep. (V)	18·9–19·5	22·0	17–40	2·24	0·21
,,	,,	July–Sep. (L) May (V)	19·8–20·4	19·3	15–35	5·0	0·47
,,	,,	May (L), June (L) Apr. (V), Oct. (V)	20·8–21·7	18·1	13–26	6·6	0·64
,,	,,	Apr. (L), Oct. (L) Nov. (L), Nov. (V) Dec. (V)	21·9–22·6	16·7	11–26	6·86	0·54
,,	,,	Dec.–Feb. (L) Jan.–Mar. (V)	22·9–23·6	14·7	11–23	6·17	0·49
,,	,,	Mar. (L)	24·1	13·0	11–23	4·71	0·75

(L) = in Laboratory; (V) = on enclosed verandah.

22·5°, 27·7 days. This last figure is in close agreement with that found in the laboratory when the temperature averaged the same, but had a range of about 3·5°. At the higher constant temperatures the duration is longer than would be expected.

I believe that the duration of the nymphal stages, under the conditions in which they were kept in the laboratory, approximates closely to that under field conditions. Twenty nymphs, hatched on 22.ix.36, were put on a branch of a coffee plant bearing leaves and green berries and kept completely unprotected out of doors. The branch was placed in water and changed every few days. Only six survived to become adult, the rest having disappeared. The average time from hatching to adult of these six was 55 days, the extremes being 48 and 59 days. Twenty-two nymphs, hatched on the same day and kept in the laboratory, all survived to maturity. The average period was 54·5 days, the extremes 48 and 63 days.

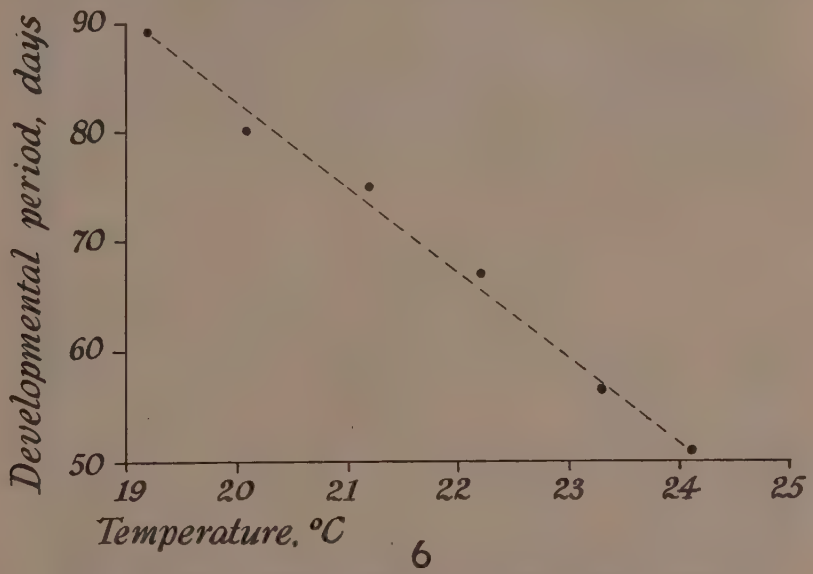

Fig. 6.—The period of development from egg to adult of *Antestia lineaticollis*, according to the temperature.

In coffee plantations both nymphs and adults avoid positions exposed to the sun during the middle of the day. Most remain in the interior of the bush or on the shaded side of berries or leaves. In the early morning and the evening, and throughout cool sunless days, they are more often found on exposed parts of the bush. When nymphs are approached they usually dodge round to the other side of the berry or leaf on which they are sitting, or hide in a cluster of berries. Adults when disturbed sometimes drop to the ground, but they often fly away, especially in warm and sunny weather. But they seldom, if ever, fly unless disturbed.

Under field conditions females are rather more numerous than males. Wilkinson, in Uganda, found 42·5% males and 57·5% females. At Lyamungu, in Tanganyika, I found 38·6% males and 61·4% females. Both Wilkinson and I have found that among bugs bred in the laboratory the proportion of males is somewhat higher, Wilkinson's figure being 52·4% and mine 48·6%.

The period that elapses from the female becoming adult to laying its first eggs is given by Wilkinson, at Kampala, as 8 to 16, with an average of 13 days.

Anderson, at Kabete, recorded 13 to 36 days, with an average of 19. The latter is in close agreement with my own records at Amani.

Wilkinson concluded that copulation took place during the night. I have myself never seen *A. lineaticollis* copulate before 16 h., but from then until dusk they frequently do.

The average duration of adult life is shown in Table 6. It will be seen that females tend to live rather longer than males. Both Anderson and I have recorded bugs of both sexes that lived for more than twice the average period. Thus Anderson kept a female alive for 290 days and a male for 249 days, and I have recorded 245 and 322 days respectively. This last figure is quite exceptional; the bug was, moreover, stylopised; it contained one male *Corioxenos*, yet it lived for 281 days after the emergence of this parasite (cf. Part III, Section 3). The next longest-lived male kept by me lived only for 197 days.

The duration of life recorded by Gowdey and Wilkinson in Uganda is surprisingly short. Hargreaves (1930, 1936), however, though he does not quote an average figure, states that in Uganda adults may live for eight months, which is in much closer agreement with other records.

The complete life-cycle, in the various localities where it has been observed, is summarised in Table 6.

TABLE 6.

Summary of the life-cycle of *A. lineaticollis*.

Authority	Locality	Time of year	Average number of days from egg to adult	Average duration of adult life		Average number of eggs laid by each female
				Males	Females	
Gowdey	Kampala	Mar.–July	84	16	16	—
Wilkinson	Kampala	Sep.–Nov.	55	—	—	—
,,	,,	Nov.–Feb.	64	57	57	106
,,	,,	Feb.–Apr.	52	—	—	—
Anderson	Kabete	Jun.–Dec.	128	—	—	—
,,	,,	Sep.–Apr.	84	106	131	126
Kirkpatrick	Amani	Apr.–June	77	103	127	148
,,	,,	July–Sep.	72			
,,	,,	Oct.–Nov.	62	98	121	
,,	,,	Dec.–Mar.	56			

It is naturally difficult to say how the length of life in the laboratory compares with that in the field. I have kept adults on a coffee bush, covered with mosquito netting but otherwise fully exposed to the weather, and more than half survived for three months and many for six months.

The foregoing account refers to *A. lineaticollis*, but so far as my observations go the life-history and habits of *faceta*, *trivialis* and *falsa* are exactly similar except in the following minor particulars. The duration of the nymphal stages of *trivialis* and *falsa* is on the average a few days longer, and of *faceta* a few days shorter, than of *lineaticollis*. But my records, especially of the earlier stadia, are insufficient to be quite certain that the difference is significant. Both *faceta* and *trivialis*, in contrast to *lineaticollis* and *falsa*, will copulate readily at any hour of the day. The feeding habits of these three species appear to be exactly the same as those of *lineaticollis*. These are discussed in the following section.

(3) Food and Feeding Habits.

(a) *Host plants.*

All authorities are agreed that arabica coffee is the principal host plant of *Antestia*. Hargreaves (1936) has recorded it living and breeding on three species of *Canthium* (Rubiaceae), but states that "the bug shows no preference for *Canthium* in the vicinity of *Coffea arabica*." He has also on one occasion found a few nymphs on robusta coffee, but considers that it cannot be regarded as a food plant. I have failed to keep either nymphs or adults alive for more than a few days when they were provided only with robusta berries. LePelley (1934) has found *A. lineaticollis* breeding on *Psychotria nigropunctata* Hiern (Rubiaceae) in the Kiambu district of Kenya.

Both Gowdey (1918) and Wilkinson (1924) record having found the bug on several other plants besides coffee, but, as the latter author states, there is no evidence that it was feeding on any of them. It can, I think, be considered certain that *Antestia* will breed only on plants of the order Rubiaceae, and that arabica coffee is by far the most favourite host plant.

(b) *The parts of the coffee plant on which* Antestia *feeds.*

Some divergence of opinion has been expressed concerning the parts of the coffee plant on which *Antestia* is able, or prefers, to feed. Gowdey (*loc. cit.*) stated that "they suck the berries, the newly set as well as the well-developed berries. . . . When neither flowers nor fruit are available the newly hatched nymphs seem to prefer the foliage, though they will also puncture the tender shoots, such as suckers. . . . Although I have reared the bug to the adult stage exclusively on tender leaves, there is no doubt that flowers and fruit are preferred, and they can only with difficulty be nduced to feed on mature leaves."

Anderson (1919) wrote: "The favourite food of the adult is the green berry [he does not state of what age]; if these are not available the buds are next attacked; nourishment can also be obtained from the delicate green twigs; the leaves are the last resort; I have not been able to keep the adult bugs alive for any length of time, on leaves (young or old) alone."

Wilkinson (*loc. cit.*) said that "there is a remarkable preference for the developing green berry. . . . Next to green berries the delicate shoots are the favourite feeding place especially at, or near, a node, that is, the part of the twig from which a pair of leaves spring. . . . The leaves are the last resort. That food can be extracted from the leaves is shown by the fact that adults have been kept alive for several weeks on leaves only, both young and old, whereas adults given no food at all died within two days. Adults have also been kept alive on ripe berries but not on berries when the bean was almost solid and the skin green and hard, which is the condition just previous to the berry becoming ripe."

Hargreaves (1936) wrote: "The feeding habit of the adult is much the same as that of the nymph; young berries in which the beans are still soft being preferred. Ripe berries also are attacked, but the beans are then too hard for the bug's proboscis to penetrate, and no appreciable damage is done to the crop. . . . Feeding experiments have indicated that berry-food is essential for the reproduction of the bug, and that egg-laying is most prolific during the first four months of the development of the berry, while the beans are still soft. After this stage (in the presence of an even-aged crop) bug reproduction falls off. . . . The more nearly mature and ripe

berries are also attacked by the bug, but the feeding appears to be restricted to parts other than the seeds. Flower buds may also be sucked. In the absence or scarcity of berries, the young shoots are liable to attack."

Notley (*in litt.*, 1936) stated that in Kenya Naismith-Jones "had no difficulty in raising *Antestia* from egg to adult on leaves and stems only, though the death rate was, he thinks, higher than on cherry. He found that the secret of raising *Antestia* is to supply any amount of water: spraying the leaves thoroughly with water as much as three times a day during hot weather was best."

In all my own experiments, apart from those detailed in this section, I have fed the bugs of all stages exclusively on full-sized but still green berries of which the endocarp (parchment) was already hard. In many, though not all, of the berries used the endosperm (bean) had become white and "cheesy," which is the condition it assumes shortly before the berry begins to turn red. Water was given to some of them during the dry season, but was found to be unnecessary. With this food I have reared several thousand bugs from egg to maturity and oviposition. The mortality, calculated from 30 egg-batches (but excluding two of which all the nymphs died within 24 hours of hatching, *i.e.* before they had fed), was about 15% during the first stadium, about 5% during the second, and about 3% during each of the third, fourth and fifth stadia. Thus nearly 75% of the bugs that hatched survived to maturity.

In the experiments of Wilkinson (1924), in which apparently young green berries were given as food, of 617 nymphs that hatched 13, 33, 22, 12 and 8% died during the respective five stadia, and only 37% became adult.

Seeing that my own experience differed from that of former workers, I made a few simple experiments on the influence of different parts of the coffee plant on development, reproduction and longevity.

(c) *The effect on the life-cycle of* Antestia *of feeding them on different parts of the coffee plant.*

Table 7 compares the life-cycle when the food given was (*a*) full-sized green berries, about four to six months after flowering, of which the parchment was hard, (*b*) half-grown green berries, about two to three months after flowering, of which the parchment was still soft, (*c*) ripe red berries. (At Amani, the berry is ripe about seven months from the date of flowering.) Ten egg-batches were used, three nymphs from each being fed on each of the three classes of food (two extra on the ripe berries). The bugs were kept in the laboratory, each separately, all other conditions were similar and no water was given.

The duration of the first stadium was the same, eight days, for all the bugs. The small amount of food taken towards the end of the first stadium has, therefore, no effect on its duration.

Premature deaths, before the bugs became adult, are shown in Table 8. The only figure significantly * different from the normal mortality is that for the large number of deaths during the second stadium of the nymphs fed on young green berries.

* To verify this, I repeated this part of the experiment during a warmer time of the year. Twenty-five nymphs moulted to the second instar on 29.xii.36. (*a*) 12 of these were fed on old green, and (*b*) 13 on young green berries. Of (*a*) 1 died during the second stadium, which was completed by the 11 survivors in 9 days (2), 10 days (3) and 12 days (6). Of (*b*) 10 died during the second stadium, which was completed by the 3 survivors in 11 days (1) and 14 days (2).

It is clear from Table 7 that full-sized green berries were a more suitable food than either ripe or young berries, for when either of the two latter were fed the period of development was increased, the length of adult life decreased, and the fecundity of the females greatly reduced. In each case the difference was statistically significant.

TABLE 7.

The influence on the life-history of *A. lineaticollis* of feeding them on coffee berries of different ages.

Nature of food	Mean duration of stadia						Av. duration of adult life		Av. no. of eggs laid by each fertilised female
	1st	2nd	3rd	4th	5th	Aggregate	Males	Females	
(*a*) Old green berries .	8·0	14·1	12·8	14·5	20·7	70·1	113	132	140
n = . .	24	23	22	20	19	19	8	11	8
(*b*) Young green berries	8·0	16·7	16·2	19·2	28·4	88·8	34	84	12
n = . .	26	15	15	13	10	10	5	5	4
(*c*) Ripe red berries .	8·0	17·2	19·3	20·5	25·4	90·4	53	78	40
n = . .	29	28	27	26	25	25	11	14	9
Difference between means of (*a*) and (*b*) .	0·0	2·6	3·4	4·7	7·7	18·7	79	46	128
Standard error of difference between means .	± 0·0	± 1·70	± 1·23	± 1·10	± 2·42	± 3·10	± 15·6	± 20·9	± 16·3
Difference between means of (*a*) and (*c*) .	0·0	3·1	6·5	6·0	4·7	20·3	60	54	100
Standard error of difference between means .	± 0·0	± 0·96	± 0·85	± 1·09	± 1·20	± 2·93	± 16·5	± 10·3	± 18·4

TABLE 8.

Deaths of *Antestia* during the nymphal stadia.

Nature of food	Number of eggs hatched	Deaths during					Survived to adult instar
		1st stadium	2nd stadium	3rd stadium	4th stadium	5th stadium	
(*a*) Old green berries .	30	6	1	1	2	1	19
(*b*) Young green berries .	30	4	11	0	2	3	10
(*c*) Ripe red berries .	32	3	1	1	1	1	25

The experiment was repeated (for the duration of the nymphal stadia only) during a slightly cooler time of the year, with a smaller number of bugs. The results were very similar and again showed a significant difference in favour of (*a*) old green berries over (*b*) young green and (*c*) ripe berries. The mean developmental period for five bugs fed on (*a*) was 77·6 days; for three fed on (*b*), 93·0 days; and for nine fed on (*c*), 95·0 days. Comparing these means by the method described by Fisher (1928 : 107) the difference between (*a*) and (*b*) is 15·4 days; $t = 4{\cdot}45$, which for $n - 2 = 6$ gives a value for P of less than 0·01. Similarly the difference between (*a*) and (*c*) is 17·4 days; $t = 5{\cdot}2$, which for $n - 2 = 12$ is nearly double the corresponding 0·01 value of P.

In order to learn whether the bug actually feeds on the hard bean or only on the pulp, I fed a pair of fourth-instar nymphs on beans from full-sized green berries, from which all the skin and pulp was removed. Water was supplied daily. These nymphs became adult and the female laid eggs. There was a large mortality among the young nymphs (fed in a similar way), but three survived to the fourth instar and one to the fifth. Of another batch of eleven nymphs fed in the same way, nine died during the first stadium, two survived to the fourth stadium and one became adult, but died 18 days later. Although, therefore, I was unsuccessful in raising a complete generation from egg to egg on beans only, it is clear that the bugs are able to extract nourishment from them.

Additional proof of this was obtained from the following experiments :—

(1) 24 lots, each of five green coffee berries, were weighed to the nearest centigram. The berries were full-sized, the endocarp hard, and the endosperm white and cheesy. To reduce the loss of weight from evaporation during the course of the experiment, the berries were kept for 48 hours after being picked before they were weighed. The average weight of each lot was then 5·33 grams. On each of 12 lots 10 adult *Antestia* were placed; no water was supplied. The remaining 12 lots were kept under otherwise identical conditions as controls. After 48 hours they were weighed again. The controls had lost an average of 13·9% of their weight, and the berries that had been fed on 22·2%. The standard error of the difference of 8·3% was 0·59.

(2) From 10 lots each of 5 similar berries all the skin and pulp was removed. The average weight of each lot was then 3·47 grams. After 48 hours 5 controls had lost 16·5% of their weight, and 5 lots fed on, each by 10 adult bugs, 26·5%. The standard error of the difference of 10·0% was 1·5.

(3) Bugs were also enclosed with weighed quantities of the skin and pulp removed from similar green berries. The average increase in loss of weight of the lots fed on over the controls was 2·0% after 48 hours, but this was not statistically significant.

Judging, however, from the appearance of the excreta I think that the bugs can extract a small amount of nourishment from the pulp in the absence of the bean.

To ascertain whether *Antestia* has any preference for berries of different ages, I kept twenty (four of each instar from the second to adult) together in one cage, and supplied them with full-sized green berries, half-grown green berries, and ripe red ones. Twenty-five observations were made at different times of the day, during a period of twenty days, and Table 9 shows the average, maximum and minimum numbers observed to be sitting on each class of berry. Though I cannot be certain that all the bugs sitting on a particular class of berry were actually feeding, the results are a strong indication that they prefer nearly mature green berries.

I have failed to keep either nymphs or adults alive in the laboratory when fed only on leaves, flower buds, or very young berries (about two to three weeks from flowering). These foods were kept fresh in water and changed frequently, so there is no question of their having been unsuitable because they had dried up. I have also tried, for experiments on leaves, small plants growing in pots, but on these also all the bugs died within at most fifteen days. When, however, they were kept out of doors and entirely unprotected, I have reared them to the adult stage on similar potted plants bearing leaves only. Eighteen nymphs, hatched on 22.ix.36, were placed on such a plant, and for comparison twenty, hatched on the same day, on a branch bearing

full-sized green berries only, all leaves being removed. This was kept fresh in water and changed when necessary, about every seven days. It was placed in a similar exposed position to the potted plant. From both of these many of the bugs disappeared, but the development of those that remained is shown in Table 10, from which it will be seen that development was slower on leaves than on berries.

TABLE 9.

Food preference of *Antestia*.

	The number of bugs observed to be sitting on			
	Full-sized green berries	Half-grown green berries	Ripe red berries	Elsewhere in cage
Average of 25 observations .	7	1	1	11
Maximum (at any one observation) .	13	4	3	15
Minimum . .	2	0	0	4

TABLE 10.

The development of *Antestia* on a plant bearing leaves only, compared with that on full-sized green berries.

Number of days after eggs hatched	Number and instar of bugs still remaining	
	On leaves	On berries
30	3 in 3rd; 3 in 2nd	11 in 4th; 1 in 3rd
36	1 in 4th; 5 in 3rd	2 in 5th; 7 in 4th
49	3 in 5th; 2 in 4th	2 adult; 7 in 5th
53	4 in 5th; 1 in 4th	3 adult; 3 in 5th
59	2 adult; 3 in 5th	6 adult. —
67	5 adult. —	— —

The reason why they were able to survive on leaves only when kept out of doors, but not in the laboratory, may be that in the former place the leaves were wet almost every night with dew, and frequently by day with rain, and that water is essential when berry food is not given. This is supported by observations made by Naismith-Jones in Kenya (Notley, *in litt.*, quoted above).

All the foregoing experiments were made with *A. lineaticollis* only. Though I have made no comparative trials on the effect of different foods on *A. faceta*, *trivialis* and *falsa*, I have reared all these three species from egg to egg on full-sized green berries only, without the slightest difficulty. I found, however, that *faceta* had a greater mortality during the first and second stadia than any of the other three species.

(d) *Summary and conclusions.*

Summarising the results of feeding experiments, it appears that at Amani *

* I have also successfully reared *Antestia* on old green berries at Lyamungu, though I did not make any comparative experiments there.

the most suitable food for *Antestia* is full-sized green berries, that they can exist on half-grown berries (but not on very young ones nor on flower buds) and on fully ripe ones, and also, but only in the open, on leaves.

At Kampala, in Uganda, the best food is young berries before they are half grown, and the bug will not exist on green berries of which the bean is solid, nor on leaves.

In Kenya the best results are obtained by feeding them on the younger green berries; they cannot feed on the older green berries, but they are able to do so on leaves.

Further investigations on the food habits of *Antestia* are obviously desirable, for the amount of damage done to the crop is largely dependent on the part of the coffee plant attacked.

I suggest that the apparent discrepancies might be accounted for by differences in atmospheric humidity. The climate of Amani is damper and somewhat cooler than that of Kampala, and much damper but rather warmer than that of the Nairobi district. In the absence of comparable meteorological data for the exact situations in which the bugs were bred, I should expect the saturation deficiency to be much less at Amani than at either Kampala or Nairobi. This may possibly explain why at Amani the bug readily feeds and breeds on the comparatively dry food of almost ripe beans, when it is unable to do so in the other two localities.

Moreover, Notley, as quoted above, states that in Kenya it is almost essential to give an abundant supply of water to the bugs. At Amani it is quite unnecessary to supply water when full-sized green cherries are given as food, though there are indications that it is necessary when leaves only are provided.

(4) The Damage Caused.

As described in Section 3, different views have been expressed concerning the part of the coffee plant most usually fed on by *Antestia*. It is therefore not surprising that there is an almost equal diversity of opinion on the nature of the damage done. It will be convenient to discuss this question under the following heads :—

(a) *Damage to the flower buds, with consequent failure of the flowers to set, or shedding of the young berries.*

Gowdey (1918) stated that "there is no doubt that the Variegated Bug is responsible for the non-setting of flowers," though he emphasises that it is only one of several causes. Anderson (1919) also considered that "next to green berries the developing buds are the favourite feeding places. The puncturing of the buds retards their development with the result that fewer flowers are formed and there is a corresponding reduction in the amount of fruit produced."

Wilkinson (1924) "is prepared to admit that *Antestia* may prevent a certain number of flowers from setting, or may cause small berries to fall, but the loss from these causes is almost negligible as compared with other forms of damage."

Hargreaves (1930, 1936), though he mentions that flower buds may be sucked, does not refer to any damage done to them, or to resulting berry fall.

LePelley (1932) in describing the abortion of flowers caused by *Lygus simonyi* Reut. [= *Lygus coffeae* China] discusses other causes that produce similar results, but does not mention *Antestia* as one of them.

My own opinion, based on observations in the districts of Kiambu, Moshi and Amani, is that *Antestia* seldom sucks flower buds except in the absence of all berries of whatever age. Whether it then causes abortion or shedding I am unable to say for certain, but believe that it does so, if at all, only to a negligible extent. I have, at Amani, liberated large numbers of adult *Antestia* on to a small coffee bush bearing flower buds but no berries, but within a few days all left the bush for a neighbouring one on which there were berries, and I found no trace of damage to the buds. I have only once (in Kiambu) found *Antestia* common on bushes that were bearing numerous flower buds but no berries. Much damage was being done to the buds, but most of it without any doubt by *Lygus*, which was also abundant. It is, however, possible that *Antestia* may have contributed to the damage.

(b) *Damage to the developing berry.*

Gowdey (*loc. cit.*) stated that " by sucking the berries—the newly set as well as the well-developed berries—it causes them to drop." Anderson (*loc. cit.*) also believed that berry-fall is caused " especially when the stalks have been attacked." Ritchie (1929) has recorded serious berry-fall thought to be caused by *Antestia* and accentuated by dry weather. Hargreaves (*loc. cit.*) makes no mention of berry-fall. I have often seen nymphs, especially of the second and third instars, apparently feeding on the pedicel of a berry, but I have no proof that berry-fall is thereby caused.

It is generally agreed by all the authorities I have quoted that the principal damage to the developing berry is caused by the bug sucking the endosperm. This results in the bean becoming spotted and pitted and, if the attack has been severe, small and shrivelled. I have stated in Section 3 that *Antestia* is, at least at Amani, quite capable of sucking the beans contained in berries of which the parchment (endocarp) is hard and the bean (endosperm) semi-solid. Such beans, when fed on, become discoloured just as the younger beans do. If a large number of bugs feed on a young berry, the endosperm is sucked practically dry within 24 hours.

(c) *The transmission of* Nematospora *spp.*

The damage done to the bean is greatly intensified when *Antestia* introduces one or both of two species of the fungus *Nematospora*. Wallace (1930, 1931) proved experimentally that *N. coryli* Pegl. was carried by *A. lineaticollis*. He has recorded that on one plantation in the Moshi district as many as 295 out of 300 berries were attacked. Subsequently (1932, 1932*a*) he found that another species, *N. gossypii* Ashby and Nowell, was equally destructive, and that at Moshi both species occurred together. He also recorded *N. coryli* from Kenya and Uganda.

Probably one or both species are widespread wherever *Antestia* is found. They are not, however, universally present, or at least not at all seasons of the year, for I have examined berries from a plantation near Lyamungu on which *Antestia* was abundant, and though many of the beans showed signs of having been fed on, very few had internal bean rot.

Nematospora can be transmitted by nymphal as well as by adult *Antestia*. Besides *A. lineaticollis*, *A. faceta* and *A. trivialis* certainly, and I suspect also the other species, are vectors.

Infected beans rot very quickly; two days after a bug has first introduced the fungus a considerable part will be brown, a few days later the whole bean

becomes rotten and stinking, and subsequently it shrivels. Infected beans are not only valueless in themselves, but may taint sound ones.

(d) *Damage to the foliage.*

Anderson (1919) stated that " sometimes when the terminal buds are punctured the shoots die back for some distance. This might mean that not only does the bug pierce but at the same time injects something into the puncture." There are, however, no indications that the saliva of *Antestia* is toxic to plants, like the saliva of some Capsidae (Smith, 1920), and fungi of the genus *Nematospora* can, so far as is known, only become established in seeds and fruits (Ashby and Nowell, 1926). Dieback is not mentioned by either Gowdey, Wilkinson or Hargreaves.

All these authorities are agreed that attack by *Antestia* near the growing point of young shoots results in the production of numerous secondary and tertiary branches. Thus Wilkinson (1924) wrote : " Bug attack on the young shoots results in the production of masses of leaves and branches with short internodes until the whole bush may present a matted appearance. These matted branches seldom, if ever, bear fruit until thoroughly pruned, or cut back, and naturally the pruning of such trees becomes increasingly difficult. Although this has not been experimentally produced, it is a phenomenon observed on most estates where *Antestia* is present as a pest and in the opinion of the writer it is the result of *Antestia* attack. At the same time it appears to be a characteristic of not a few coffee bushes in Uganda to present a similar matted appearance after the rains and before pruning has been done. This characteristic was not observed by the writer in Kenya. About the only reliable difference which could be pointed out as distinctive is the broader and more flattened appearance, dorso-ventrally, of the nodes in the case of bushes suffering from bug attack. This broad, flat, character of the nodes has already been observed by many planters and, I think rightly, put down to *Antestia*."

Smee (1931) has recorded *A. variegata* Thunb. [? = *faceta* Germ.] as producing in certain districts of Nyasaland " a very pronounced vegetative growth and a complete absence of crop. . . . The shoots were marked by abnormally short internodes . . . and a proliferated growth of secondaries or tertiaries from each node. . . . By caging specimens of the insects on apparently healthy coffee trees proof was obtained that [*Antestia*] was alone responsible."

I myself have failed to produce this condition experimentally, although I have kept very large numbers of *Antestia* for several months on a small coffee bush enclosed in mosquito netting. However, in order to keep them alive and stimulate breeding, branches bearing green berries were enclosed in the cage, and it is quite likely that the bugs fed scarcely at all on the growing plant. I have also seen coffee plantations, in both the Kiambu and Moshi districts, where although *Antestia* was exceedingly abundant this matted appearance of the branches was absent. I think, however, that the condition is produced by *Antestia*, but probably not unless the plantation has at some time of the year been almost devoid of berries, so that the bugs have been compelled to feed on the leaves and young shoots. It would be very desirable to obtain, if possible, further experimental proof of the connection of *Antestia* with this " witches' broom " appearance, which on some plantations is undoubtedly responsible for a large reduction in the crop.

(e) *Summary.*

Summarising my own opinions on the injuries caused by *Antestia*, the principal damage is due to the bugs sucking the developing berry and producing spotted and pitted beans. The younger the berries attacked, the greater is the harm done. If *Nematospora* is introduced, the bean is completely destroyed. In the absence of berries the young shoots are attacked, and a mat of short secondary and tertiary branches, which bear no crop, may be the result. The conditions under which this form of damage is produced require further study.

(5) Eco-climatic Factors affecting abundance.

In East Africa arabica coffee is grown at all altitudes between about 3000 ft. and 7000 ft., and, therefore, under widely varying climatic conditions. Yet in most districts *Antestia* is, or at times has been, abundant.

I have shown (Kirkpatrick, 1935) that there are several distinct eco-climates in different parts of a single coffee bush. *Antestia* is a mobile insect, and therefore at liberty to choose that part of the bush in which it finds the most suitable conditions. That it actually does so, at least to some extent, I have observed on many occasions. Thus it is very seldom that *Antestia* can be found on exposed parts of unshaded bushes either in the middle of sunny days, when the outer parts of the bush are warmer than the interior, or on clear nights when they are colder. On the other hand, in the early morning and evening, and on cool cloudy days even at midday, they can often be seen on the surface of the bush, exposed to such radiant heat as there is. To some extent the presence of suitable berry-food must determine the part of the bush they frequent. I have, however, shown, at least in the laboratory, that they spend less than half the day sitting on their food (Table 9 in Section 3), and therefore probably a still shorter time actually feeding.

Consequently at first sight it seems that eco-climatic factors can have but little influence on the incidence of *Antestia*; this also appears to be supported by the apparently contrary opinions that have been expressed about the effect of shade. Thus Anderson (1925) considered that less damage was done to properly shaded coffee. Hargreaves (1924) gave it as his tentative opinion that absence of shade increased the numbers of the bugs and the damage done by them. Wilkinson (1924*a*) also said that " *Antestia* even when present in large numbers appears to cause little damage under shade."

On the other hand, Hargreaves (1929), referring to Toro, a different district of Uganda from that where his previous observations were made, wrote : " In most cases shade was probably responsible for the attack; with the removal of shade trees the pest disappeared . . . probably as a direct result of removal of protection of the bug from the effects of cold nights which are normally experienced in Toro."

I believe that shade may have the same effect in low-lying and hot districts. On a plantation near Moshi, at the lower limit of coffee cultivation (about 3500 ft.), I have found the bug much more common under shade than in an adjacent unshaded plot. I have, however, only made this observation at two seasons of the year (January and May) and only by visual estimation, not by the accurate method of spraying a number of trees, as recommended by LePelley (1934*a*).

I suggest that the foregoing observations, so far from being contradictory,

tend to show that in any one district eco-climatic factors exercise an appreciable influence on the abundance of *Antestia*. At higher altitudes, where the nights are in any case cold, it is more numerous in the less cold shaded plantations. If my own observations, which admittedly require confirmation, are correct, *Antestia* also requires the protection of shade at the other climatic extreme—at low altitudes where the day temperature is exceptionally high. In the intermediate districts it thrives best in unshaded plantations where the higher day temperatures probably have more effect in increasing the rate of reproduction than the higher night temperatures in shaded plantations.

Another important effect of shade is to raise the humidity of the air by day and to lower it slightly at night, and also to decrease considerably the deposition of dew (Kirkpatrick, *loc. cit.*). Wilkinson (1924) has adduced some evidence that *Antestia* tends to increase during a period of dry weather. Hargreaves (1930) has observed that " continuous clean weeding of the soil renders the coffee more liable to attack by *Antestia*." I have shown (*loc. cit.*) that weeds or a cover crop increase the humidity of the air. Much of the beneficial effect of shade (as of cover crops) may therefore be due to the higher humidity by day, and quite possibly to the less frequent deposition of dew at night. For even though *Antestia* thrives well in a dry atmosphere there is evidence (discussed in Section 3) that it then requires moisture to drink. Again, I have in Section 3 put forward the hypothesis that in a drier atmosphere *Antestia* prefers to feed on young juicy berries, and under damp conditions on the more mature ones. The younger the berries fed on, the more damage is done; this would therefore account for the statements quoted above that, even when the bug is abundant, it does less damage under shade.

Anderson (1918) quoted a statement that more damage was done close to a *Grevillea* wind-break. Trench (1926) also wrote: " It has been observed that where wind-breaks have been allowed to get too thick or dense, that the outbreak of insect pests, such as *Antestia* and Thrips, are most prevalent."

A possible explanation might be the slightly higher day temperature caused by wind-breaks. I think, however, that it is more likely to be due to the competition of the *Grevillea* accentuating drought conditions. Trench (*loc. cit.*) has stated that " during long spells of dry weather, the coffee bushes have suffered from lack of moisture, due to the *Grevillea robusta* taking more than its share."

I should expect that *Antestia* would tend to multiply less rapidly in bushes that are kept well pruned than in ones that have abundant thick foliage, because in the former the day temperature will be rather lower and the evaporation-rate higher. For the reasons already given this would probably not apply to low-lying hot districts nor to cold exposed plantations at high altitudes. Bushes grown on the multiple-stem system would be subject to conditions similar to those of fairly well-pruned single-stem bushes.

I believe, however, that the direct influence of climate is of minor importance compared with its indirect effect through the host plant. It is certain (Section 3) that *Antestia* reproduces most rapidly when green berries are available as food, though in some districts very young berries and in others older ones may be the more suitable. Consequently the *Antestia* population is most likely to remain at a high level where the climate (and the system of pruning adopted) favours several flowerings during the year. Drought conditions may in themselves increase the population and further, as suggested by Ritchie (1929), it is very probable that more damage is done to the crop on bushes suffering from lack of moisture.

(6) Natural Enemies.

(a) *Hymenoptera. Egg-parasites.*

Two species of Scelionidae, *Microphanurus seychellensis* Kieff., until recently known as *Telenomus truncativentris* Dodd (Nixon, 1935), and *Hadronotus antestiae* Dodd (1919) are found in almost all districts in East Africa where *Antestia lineaticollis* occurs. In Nyasaland only the former species has been recorded (Smee, 1930).

Their life-histories have been described by Anderson (1919) and Dry (1921) and need not be repeated in detail here.

One or both of these parasites is usually abundant. Dry (*loc. cit.*) found that at Kabete in Kenya they were about equally common; the percentage of eggs parasitised by one or the other varied from 54 to 90 with an average of 77. Wilkinson (1924) recorded 95% parasitised in one district of Uganda and 40% in another; *Hadronotus* was the more numerous. No actual counts of the percentage of parasitism appear to have been made elsewhere, but Ritchie (1932) stated that in Tanganyika both species are " universally present but alone effect a control which permits of too great depreciation of crop."

Anderson (1936) recorded both species from the eggs of *A. faceta* in Uganda; though it appears not to have been observed, I think it probable that they would also attack other species of the genus.

Dry (*loc. cit.*) found that *Hadronotus* was the more prolific; the average number of offspring produced by each female was 51 when fed and 23 when unfed. *Microphanurus* averaged 22 and 7·5 respectively. The life-cycle, from egg to adult, of *Microphanurus* was shorter than that of *Hadronotus*, especially in cool weather. The variation recorded was: for *Microphanurus*, 21 days in February (average temperature 19·2° C.) to 46 days in July and August (average temperature 15·2° C.); for *Hadronotus*, 24 days in February to 62 days in July and August.

This may indicate that under warm conditions *Hadronotus* is likely to be the more abundant species.

Another species of *Microphanurus*, *M. suranus* Nixon, may also be an egg-parasite of *Antestia* in Uganda. Nixon (1936) described this species from three females bred by Gowdey in 1916 " presumably from hemipterous eggs; these females were evidently bred with a series of *Microphanurus seychellensis* Kieff."; and from a pair bred by Hargreaves in 1929 " from hemipterous eggs on coffee."

Two varieties of the Eupelmid, *Anastatus bifasciatus* Fonsc. have been bred from the eggs of *A. lineaticollis* in Uganda by G. L. R. Hancock. These have been named by Ferrière (1930) var. *antestiae* and var. *hancocki*. There appears to be no experimental proof that they are not hyperparasites, but most species of this genus are primary parasites.

Species of three other genera, *Aprostocetus* (Chalcididae), *Baryconus* (Scelionidae), and *Pleurotropis* (Eulophidae), have been bred from eggs of *A. lineaticollis* in Uganda, the two former by Hancock (1926) and the third by Hargreaves (1927). It is presumed that these species are hyperparasites, for the latter author states that attempts to parasitise *Antestia* eggs with any species except *Telenomus* [*seychellensis*] and *Hadronotus antestiae* were unsuccessful.

(b) *Hymenoptera. Parasites on the nymphs.*

Helorimorpha coffeae Brues (Braconidae).

This species was described by Brues (1924) from specimens collected in Kenya. It was then thought to be parasitic on a fruit-fly, but it has since been bred by LePelley in Kenya from both nymphs and adults of *A. lineaticollis* (Wilkinson, *in litt.*, 1936).

In July 1936 Mr. B. Cooper brought to Amani a number of immature *Antestia* collected in the Marangu district, on the south-east slope of Kilimanjaro.

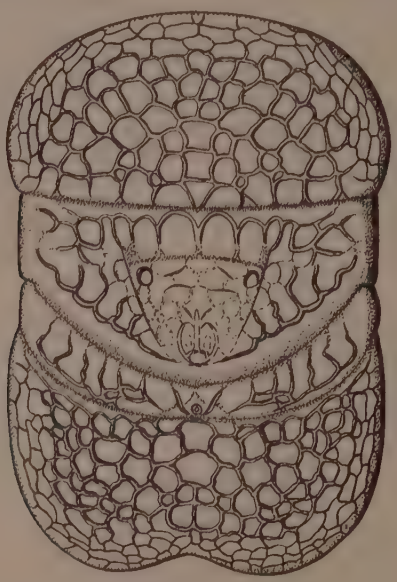

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Fig. 7.—*Helorimorpha coffeae.* Thorax and propodeum. × 57.

Several larvae emerged from these, but only three adults were obtained. Mr. H. Wilkinson kindly compared these with his named specimens of *H. coffeae* and confirmed my identifications. Since it appears not to have been figured, I give a drawing of the thorax and propodeum (fig. 7), for comparison with that of the next species. Unfortunately the only female I obtained died almost immediately, so I was unable to breed this species in the laboratory.

Helorimorpha ? sp.

From some nymphs of *A. lineaticollis*, collected in August 1936 on a plantation near Lyamungu, I obtained several larvae which were successfully bred to adult. Pending identification by the Imperial Institute of Entomology, I assign these provisionally to the genus *Helorimorpha*. The adult is 4·0 mm. in length, thus slightly smaller than *H. coffeae*, from which it is easily distinguished by the greater part of the dorsum of the thorax (but not the propodeum), and the sternum between the front and middle coxae, being almost black. The

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FIG. 8.—*Helorimorpha* sp. Thorax and abdomen. × 52.

areolation of the thorax and propodeum (fig. 8) is very similar to that of *H. coffeae* (fig. 7); the wing venation (fig. 9) is almost identical in the two species. I have found this species easy to breed in the laboratory; the following preliminary notes on its life-history may be of interest.

Oviposition. The female prefers to oviposit in second and third-instar nymphs. It will oviposit in first-instar nymphs, but apparently these then die prematurely; also in fourth-instar nymphs, if no others are available. I have watched it attempt to lay eggs in nymphs of the fifth instar, but it never succeeded, except in one that had just moulted and was still soft. It has also oviposited in an *Antestia* that had just moulted to the adult instar, but it will not even attempt to lay eggs in adults of which the integument has hardened. The female usually approaches from behind and feels the dorsum of the nymph

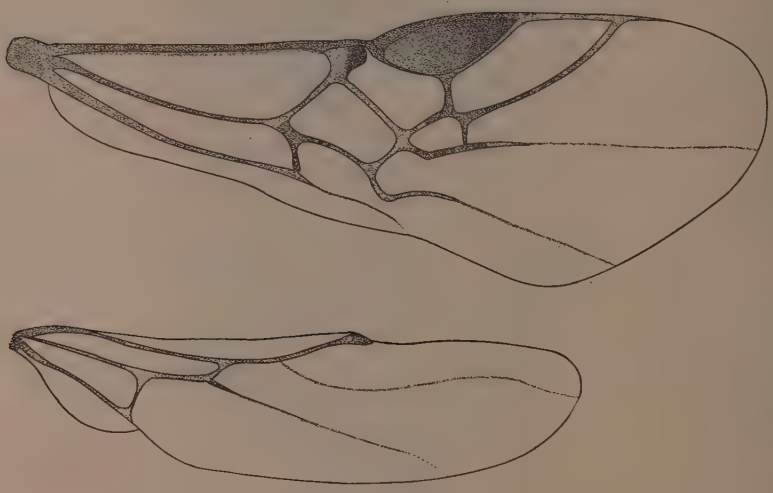

Fig. 9.—*Helorimorpha* sp. Wings. × 46.

with its antennae. It then quickly bends its abdomen forwards under the thorax and between the legs, and stings the nymph near the base of the dorsum of its abdomen. Occasionally I have watched one sting a nymph in the venter of its abdomen. The ovipositor is usually withdrawn immediately. Sometimes a female fails to sting at the first attempt; it then usually tries again at once. But even an apparently successful attempt does not always result in the deposition of an egg. Of 145 nymphs which appeared to have been properly stung, only 110, or about 75%, produced larvae. Not all the remaining 35 were examined, but in those that were, I failed to find an unhatched egg.

If plenty of potential hosts are available a female will not usually lay more than one egg in each. I have, however, found as many as six eggs in one *Antestia*, laid by a female to which no other nymphs had been offered for several days. A female will also readily lay a second egg in a nymph that has moulted since it was first stung. But I have never found that more than one egg in each host hatched.

I have not ascertained the number of eggs that a female is capable of laying,

but I have watched one sting 25 nymphs within about 30 minutes; it would not then sting any more on that day. I have kept a fertilised female that continued to lay eggs, whenever potential hosts were offered to it, over a period of 28 days.

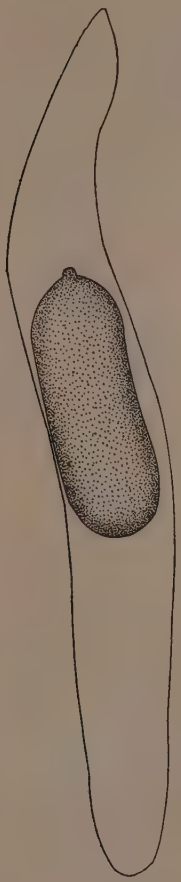

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Fig. 10.—*Helorimorpha* sp. Egg, 10 minutes after being laid. × 253.

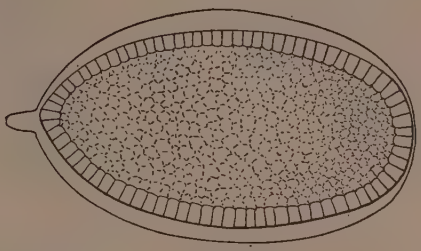

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Fig. 11.—*Helorimorpha* sp. Egg, 24 hours after being laid. × 253.

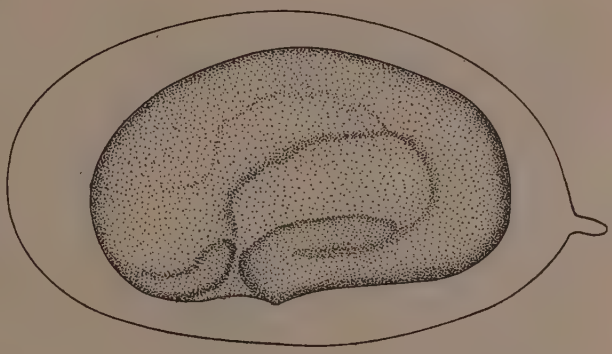

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Fig. 12.—*Helorimorpha* sp. Egg, 48 hours after being laid. × 253.

The chorion of the egg immediately after it has been laid is elongate and curved (fig. 10). A few hours later it has become oval and the embryo has swollen considerably (figs. 11 and 12). Under laboratory conditions, at a temperature ranging between 21° and 26°, the egg usually hatches 72–80 hours after oviposition.

Larva. The primary larva (fig. 13) is of the typical caudate form. Owing

to the wide variation in the time of development from oviposition to emergence of the mature larva (Table 11), I cannot say at what period the tail is lost and

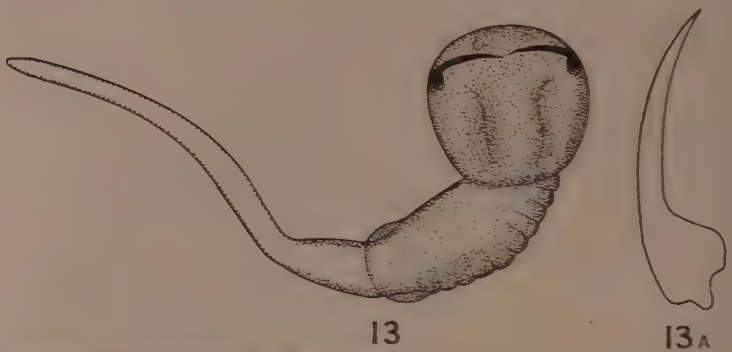

Fig. 13.—*Helorimorpha* sp. First-instar larva, shortly after hatching. × 103.
Fig. 13*a*.—*Helorimorpha* sp. First-instar larva, mandible. × 410.

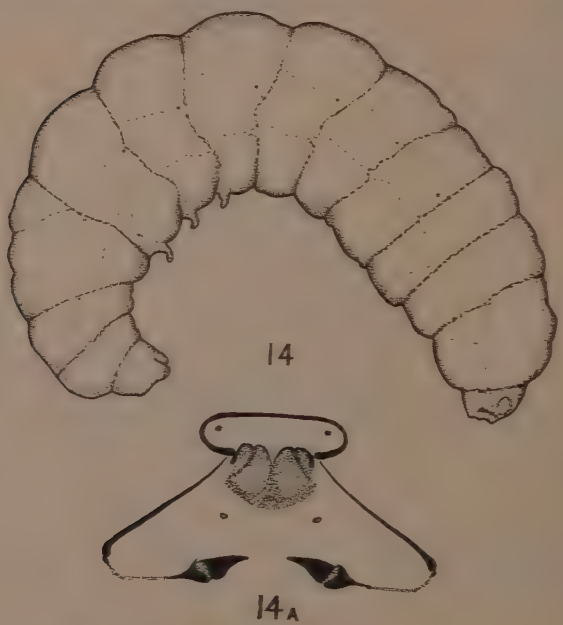

Fig. 14.—*Helorimorpha* sp. Mature larva. × 22.
Fig. 14*a*.—*Helorimorpha* sp. Mature larva, mouth-parts. × 96.

the maggot-like instar assumed. Larvae that I have examined twelve days after oviposition were still caudate and with the anal vesicle larger than in the newly-hatched larva. The mature larva (fig. 14) is white, entirely covered with very

short fine hairs; on the venter of each of the fourth, fifth and sixth abdominal segments there is a short unpaired process.

The larva leaves its host through a hole made in the abdomen, either on the dorsal or ventral surface and usually near the anus, but not through the anal aperture. The host generally dies between one and six days after the larva has emerged; a few have lived as long as nine days.

The period of development, from oviposition to the emergence of the mature larva, varies greatly even among larvae from eggs laid by the same female on one day, and in hosts kept under identical conditions. Table 11 shows the duration of this period, in days, for 333 larvae the hosts of which were kept in the laboratory at a temperature varying from a minimum of 20°–22° to a maximum of 25°–27°. Since I have occasionally found an unhatched egg in a host about two weeks after it had been stung, it may be that delayed development is due to some eggs not hatching in the usual time of about three days.

TABLE 11.

The period of development of *Helorimorpha* sp., from deposition of egg to emergence of mature larva from host.

Days	16	17	18	19	20	21	22	23	24	25	26
Instances	3	9	11	17	35	30	33	24	20	22	17
Days	27	28	29	30	31	32	33	34	35	36	37
Instances	16	14	12	11	9	12	9	6	2	3	2
Days	38	39	40	41	42	44	54	56	65		
Instances	3	2	2	1	2	1	1	1	1		

A parasitised nymph will undergo one, and sometimes two, ecdyses before the larva emerges, but delayed development of the latter apparently entails prolongation of one of the host's stadia. This is not quite certain, for it has been shown in Section 2 that the stadia of *Antestia* are occasionally, for no apparent reason, prolonged for much more than their normal duration. I do not, however, think that such prolongation of the host's stadia is the cause of the frequent delayed development of the parasite, as shown in Table 11, for the proportion of hosts of which an ecdysis has been delayed, when they have been parasitised by *Helorimorpha* sp., is much in excess of that among unparasitised *Antestia*.

Pupation. The mature larvae usually leave their hosts early in the morning, most of them before 06h. and few later than 08h. They move quite fast, always backwards, and as a rule all the time emitting a thread of silk. If loose dry earth is available they quickly burrow into it and spin a cocoon. They will also spin on the floor of their cage or on coffee berries, but in the absence of earth many die, apparently through having wasted their silk in trying to spin up in an unsuitable place. Larvae that fail to spin a cocoon by about noon on the day they emerge apparently never survive, though they may not die for another day or so. The cocoon is oval, of tough very viscous white silk. The time elapsing from spinning a cocoon to the emergence of the adult is, under conditions of temperature mentioned above, 17–19 days for males and 20–21 days for females. I have kept the adults alive for as long as 40 days in the laboratory, feeding them on dextrose syrup.

Copulation. Both sexes will copulate almost immediately after emergence from the pupa. The male, continually fanning its wings, approaches the female from behind and thrusts its abdomen under its thorax in order to effect copulation—in just the same way that a female does in order to oviposit. Copulation lasts a few seconds only but may be repeated at frequent intervals

during the first day, and occasionally on the second day, that a pair are put together. After that a male appears to take no further interest in a fertilised female.

Proportion of sexes. The offspring of fertilised females are of both sexes, females being about twice as numerous as males. Unfertilised females readily oviposit but their offspring are all males, as is usual with parasitic Hymenoptera.

Hosts. This parasite will, in the laboratory, readily breed in *A. faceta* and *A. trivialis* as well as in *A. lineaticollis*.

I have offered them young nymphs of a few other species of PENTATOMIDAE. Some of these they attempted to sting, but I could find neither eggs nor larvae in any except the three species of *Antestia* mentioned.

Multiparasitism. I have only recorded, in the field, a single case of multiparasitism, *i.e.* "the simultaneous infestation of the same individual host insect by two or more species of primary parasites" (Imms, 1931). This was a nymph of *A. lineaticollis*, from which a larva of *Helorimorpha* sp. emerged, and which, when it died a few days later, was found to contain two larvae of *Corioxenos*. Experimentally, in the laboratory, I have several times produced multiparasitism with *Helorimorpha* and *Corioxenos*. Whichever parasite entered the host first, the Hymenopteron was always the survivor.

(c) *Strepsiptera.* Corioxenos antestiae *Blair*.

I first found this species early in 1935, at Lyamungu near Moshi. The method of its discovery is of some interest. I was working on an eco-climatic problem for which large numbers of *Antestia* eggs were required. One morning I casually boxed the first specimen of *Antestia* I saw, in order to show it to my African assistant, so that he could collect the bugs for me. On returning to the laboratory I was surprised to see a living male Strepsipteron in the "pill-box." I did not at once connect the two, thinking that I had accidentally boxed the Strepsipteron without at the time seeing it. However, when the numerous *Antestia* collected by the "boy" laid scarcely any eggs, I examined a number of them and found that a large proportion was stylopised.

On the slopes of Kilimanjaro there are coffee plantations at all altitudes between about 3500 ft. and 6000 ft., and they are, therefore, subject to a wide range of climatic conditions. I found *Corioxenos* parasitising *Antestia* on all the plantations I visited, and also in the Arusha district, on the slopes of Mount Meru. It appears, however, to be restricted to these two mountains, for I have examined large numbers of *Antestia* from other districts in Tanganyika and also from Kenya (these kindly supplied by Mr. Notley) but never found a single one stylopised.

In view of the great interest of finding a Strepsipteron in a host so easily bred in captivity as *Antestia*, and moreover in a host of economic importance, it appeared worth while to devote some considerable time to a study of this parasite. The results of these investigations are given in detail in Parts II and III of this paper.

(d) *Diptera.* Epineura rubens *Villen.* (TACHINIDAE).

This was first recorded by Hargreaves (1925) from the Mitanya district of Uganda. Wilkinson (1924) stated that the percentage of *Antestia* parasitised by it was only 2½, and that from 41 larvae which left their hosts and pupated no more than six adults emerged. Larvae emerged only from adult bugs, but it is not known in what instar of the bug the egg is laid, since he was

unable to get the fly to oviposit in captivity. Wilkinson (*in litt.*, 1936) has informed me that LePelley has bred this species from adult *A. lineaticollis* in Kenya. From several hundred adult *A. lineaticollis* collected in the West Usambaras, Tanganyika, I obtained three dipterous larvae. These pupated but adults failed to emerge, so I am unable to say whether they were of this species.

(e) *Acari.*

The larva of an Erythraeid mite is sometimes found attached to adult *Antestia*, usually on the underside of the fore-wings or under the scutellum. I have never found them common, except on one plantation in the West Usambaras, where over 50% of the *Antestia* (*lineaticollis*) collected had one or more mites adhering. Several had ten or more, and one as many as 40. The bugs with such large numbers appeared to be unhealthy and to die sooner than those with few or none. It is, however, possible that the mites attach themselves more readily to *Antestia* that are old or otherwise weakened, and I am very doubtful whether they are really ectoparasites. I was unable to breed the adult mite.

(f) *Protozoa.*

A flagellate Protozoan, possibly of the genus *Leptomonas*, is often found in the intestine of both nymphs and adults of *Antestia*. In many it is absent, but if present at all it is usually in enormous numbers. I have no evidence that it has any effect on its host.

(g) *Predators.*

Antestia, like all Pentatomids, is very seldom attacked by predators. Hargreaves (1930) stated that " Mantids of undetermined species have been observed to prey on the bug," and this is the only definite observation of an insect predator on record. According to Hargreaves (1936) " It seems likely that several species of carnivorous ants such as *Oecophylla smaragdina* and *Macromischoides aculeatus* . . . play some part in the control of *Antestia*." I have myself sometimes seen ants carrying off dead *Antestia*, but have never for certain observed them to attack living ones.

LePelley (1934) records that several planters in Kenya state that *Antestia* is controlled by birds. " Droves of blue starlings regularly clear up severe attacks leaving hardly an insect to be seen." This planter " is satisfied with the control by blue starlings and uses no other." LePelley's comment is that " he is to be envied."

I am informed by Mr. R. E. Moreau, who has an extensive knowledge of East African birds and their habits, that the " blue starlings " are typically frugivorous and would be unlikely to eat insects.

LePelley (*loc. cit.*) has himself observed that poultry will follow the sprayers and eat *Antestia* as they drop to the ground, but, as he remarks, " it is obvious that they cannot influence the position on a plantation."

(7) Artificial Control Measures.

Three distinct methods for the control of *Antestia* have been widely recommended : hand collection, contact insecticides, and poison bait sprays.

(a) *Hand collection.*

This method has, until recently, been advocated by almost everyone who has offered advice about the control of *Antestia*. It has found considerable favour among planters, who are impressed by the large numbers of bugs that can be killed without any capital expenditure or much supervision. Wilkinson (1924) recommended smoking the bushes with smouldering cow-dung as an aid to collection. This causes many of the bugs to run to the centre of the bush and down the trunk. There is no doubt that if hand collecting is to be practised at all, it should be done in conjunction with smoking.

Widely different estimates of the cost of hand collection have been given by different authors. Thus Hargreaves (1936) stated that the low cost, "about five shillings per acre per year," is one of its main advantages over other methods. On the other hand, LePelley (1934) wrote: "Of the total number of insects present on trees thick in foliage, the percentage collected at a cost of Sh. 136/- per acre was 80 per cent. The best experimental results obtained was a reduction of *Antestia* by 75 per cent. on trees which had been reduced by drastic pruning almost to a condition of leafless sticks. This cost Sh. 20/- per acre."

Recently LePelley (1935) has made an experimental study of this method on coffee plantations in Kenya. He has presented his evidence in detail and concludes that "in practice the cost of picking an adequate percentage is almost invariably prohibitive."

With this conclusion, as applied to large European-owned plantations, I am in full agreement. I think, however, that on small native holdings of perhaps two or three hundred bushes, which are carefully looked after by the owner himself, hand collection (which will be done, unpaid, by his family) may still be of economic value.

(b) *Contact insecticides.*

Various contact sprays were tried by Gowdey (1918) in Uganda, the most effective of which was a resin wash (caustic soda, 4 lbs.; resin, 6 lbs.; whale-oil soap, 10 lbs.; water 45 gallons). He also stated that a nicotine spray was effective but its cost prohibitive. Apart from this suggestion contact sprays have been neither advocated nor, so far as I know, employed, until the recent experiments in Kenya on the use of pyrethrum. This was first recommended by LePelley (1932) in the form of an extract of 1 lb. pyrethrum powder in 1 gallon paraffin, used undiluted with a small "mist" sprayer. It was originally tried, and proved to be efficacious, against the Capsid *Lygus simonyi* Reut. (= *L. coffeae* China); subsequently LePelley (1932*b*, 1933) stated that in many circumstances it was also the most satisfactory method of controlling *Antestia*. He recommended its use (1) when *Lygus* is also present; (2) when the infestation of *Antestia* is particularly severe; (3) when two or three sprayings with the poison bait (discussed below) have failed to effect control. He claimed that a 95% kill should be obtained by one application of this spray, if properly applied according to his directions. (It is almost essential to cover each bush with a sheet while it is being sprayed. Either the ground under the bushes must also be sprayed after the bugs have dropped, or children must be employed to pick up the fallen bugs. If neither procedure is adopted many of the bugs recover.)

The chief drawback of pyrethrum-paraffin sprays is the high cost, about Sh. 11/- to 16/- per acre for one application. Two sprayings will usually be necessary, at least if there are many eggs of *Antestia* on the bushes.

LePelley (1933) discusses the effect of this spray on the fauna of the coffee plantation. He admits that " a large proportion of the Coccinellid and other predators of *Pseudococcus lilacinus* [= *P. kenyae*] and other insects are killed. Where *Pseudococcus* [*kenyae*] is a major pest, and it is known that it is being controlled by predators, it is probably not advisable to use this spray." Many Hymenopterous parasites, *e.g.* of *Antestia* eggs or of leaf-miners (*Leucoptera* spp.), are also killed, but since only those present as adults at the moment of spraying will be destroyed, he does not consider their loss serious.

This method is of little use during wet or windy weather, or on plantations with multiple stem bushes, the tops of which are often out of reach of a small " mist " sprayer. For such conditions Notley (1933) recommends emulsifying the pyrethrum-paraffin extract with soap and diluting with water in the proportion of 1 : 50. About one quarter of a gallon * is required for each bush.

With a dilution of 1 : 150 the bugs will fall off the bush in a comatose state, but not be killed. Children must then be employed to collect them; provided that the plantation is free of weeds, this method is slightly cheaper.

Notley estimates the cost at about Shs. 14/- per acre using the stronger concentration and Shs. 10/- with the weaker followed by collection of the fallen bugs, as compared with Shs. 16/- for the undiluted pyrethrum-paraffin extract.

Dusting with pyrethrum powder appears first to have been tried by Ritchie (1932), who stated that he obtained 100% kill but that the physical properties of the powder were unsatisfactory, and there was much wastage from pelleting.

Recently, however, Notley (1936) has recommended dusting with very finely ground pyrethrum powder. An application of 8 lbs. per acre resulted in a kill of 94·2% of *Antestia* (and 95·6% of *Lygus*). The cost is given as Shs. 5·50 per acre, or less than half that of the other methods involving the use of pyrethrum.

(c) *Poison bait sprays.*

Control of Hemiptera by means of stomach poisons is unusual, but several attempts have been made to find an efficient poison bait for *Antestia*, one of which has met with considerable success.

Anderson (1919) tried many varieties of poison baits, in most of which the toxic principle was apparently Paris Green, but the results were not promising. In 1923, Ritchie began experiments with sweetened sodium arsenite. Eventually (Ritchie, 1932) the following formula was recommended—arsenite of soda, 60 grammes; unrefined sugar, 5 lbs.; water, 4 gallons. A minimum dose of one fluid ounce is applied to each bush with a sprayer that gives an upwardly directed fine mist. Three or more sprayings may be necessary, but the cost of each is small, and Ritchie states that " *Antestia* control by this method should cost from 5 to 6 shillings per acre per annum." In the coffee plantations of the Moshi and Arusha districts of Tanganyika bait spraying has become the standard method of control, and at least the majority of planters are completely satisfied with it. It has, however, not met with the same success in Kenya and Uganda. LePelley (1932*a*) has studied the reason for this in Kenya. He made a careful estimate of the effect of poison bait

* LePelley (1934) questioned this and said that " Experience in the Kiambu district has shown that a minimum of about 1 gallon a tree is necessary with water sprays used as insecticides."

on the fauna of a coffee plantation, and concluded that the resulting destruction of the egg-parasites of *Antestia* might be the cause of some of the unsuccessful results. I have advanced the suggestion (Section 8 (*c*); see also Part II, Section 3 (*e*)) that the almost consistently good results claimed for poison baiting in the Moshi district may be explained by the fact that there the control effected in other districts by Hymenopterous egg parasites is largely replaced by the Strepsipteron *Corioxenos*.

Apart from the frequent failure of poison bait to control *Antestia* in Kenya, LePelley (*loc. cit.*) has suggested that it resulted in an increase in the numbers of injurious Coccidae and of leaf-miner (*Leucoptera* spp.), owing to the destruction of their natural enemies. Later (1934) he obtained further evidence that there was a real danger of serious outbreaks of leaf-miner following on repeated sprayings. Hymenopterous parasites readily feed on the sweetened bait, which will remain strong enough to kill them for some time after it has become diluted by rain and dew below the strength necessary to kill *Antestia*. Hargreaves also reported (1932) that in Uganda arsenic bait spray " in one instance resulted in severe attack by mealy-bug, presumably by poisoning its natural enemies."

(8) The Control of *Antestia*. Summary.

(a) *Eco-climatic and cultural methods.*

Although it is very unlikely that complete control can anywhere be obtained solely by eco-climatic or cultural methods, I suggest that the following should tend to reduce the population of *Antestia*.

(1) The presence of canopy shade, which will raise the humidity of the air by day, decrease the dew-fall, lower the day temperature, and conserve soil-moisture. But in districts where cool and damp conditions both of the air and of the soil are prevalent, these results may have little effect and may be offset by the raising of the night temperature, which in an unshaded plantation would be too low for *Antestia*. Similarly in hot dry low-lying districts shade may render the conditions more suitable for the bug by reducing the high day temperatures.

(2) Avoidance of clean weeding or, preferably, growing a cover crop. This will raise the humidity of the air, lower the night temperature, and conserve soil moisture. It is most likely to be advantageous where shade is for some reason undesirable or impracticable.

(3) Absence of wind-breaks, except where they are really necessary as a protection from high winds. Certain trees commonly used, e.g. *Grevillea*, take more moisture from the soil than they conserve by reducing evaporation, and should therefore be dispensed with, if possible, in districts liable to drought.

(4) Adopting a system of pruning that reduces " intermittent flowering " to a minimum, so that as far as possible all the crop on the bushes at any one time is in about the same stage of development. The influence of pruning at different times of the year on the time of flowering is at present being investigated in Kenya (Trench, 1936).

(b) *Biological control.*

There can be no doubt that the Hymenopterous egg-parasites and, where it occurs, the Strepsipteron *Corioxenos*, are of the greatest importance in reducing the rate of increase of *Antestia*.

I am very doubtful if any of the other recorded parasites are of much

value; possibly the species of *Helorimorpha* may at times exercise some influence in certain districts.

It has often been suggested (Anderson, 1919; Wilkinson, 1924; Hargreaves, 1930; LePelley, 1932*a*) that in order to increase the population of egg-parasites the eggs of *Antestia* should be collected, kept in suitable cages, and the emerging parasites liberated in the plantation. Theoretically this sounds an excellent recommendation, but in practice the number of egg-batches that can be collected by even the most careful searchers is a very small proportion of those present. A little carelessness in the conditions under which the collected eggs are kept, or neglect to liberate the adult parasites immediately they emerge, may well result in more harm than good being done. LePelley (1934) himself said of this procedure that it " may be completely excluded from further consideration by planters; it is valueless."

I believe that the only practical way of aiding the biological control of *Antestia* is by the choice of the most suitable method of artificial control, according to whether most of the biological control is being effected by egg-parasites or by *Corioxenos*. This is discussed below.

(c) *Artificial control.*

It has been seen that except possibly in small native holdings, hand collection as a means of control may be ruled out. There remain what can almost be described as the two rival methods—baiting with sweetened arsenic and, in some form or other, spraying or dusting with pyrethrum.

I suggest that where most of the natural control is due to *Corioxenos*, sweetened arsenic bait is, quite apart from its relative cheapness, the preferable method. For it will not kill the triungulins of *Corioxenos* that are waiting on a coffee bush until they can find a host, since they do not feed; though it will of course kill adult *Antestia* that may contain parturient female parasites, these will, while dying, continue to produce unharmed triungulins. Pyrethrum would probably destroy most of the free-living triungulins on a bush and, since it is much quicker in its action than poison bait, it is unlikely that many triungulins would escape from parturient hosts killed by it.

Where *Corioxenos* is absent and the egg-parasites are the most important natural controlling factor, pyrethrum would appear to be the more advantageous, since it destroys a smaller proportion of the egg-parasites than poison bait does.

PART II.

THE BIONOMICS OF *CORIOXENOS ANTESTIAE*.

(1) Descriptions of the Instars.

Shortly after this Strepsipteron was found specimens were sent to Sir Guy Marshall, Director of the Imperial Institute of Entomology, who passed them on to Dr. K. G. Blair for description. Blair's original description (1936) is of necessity incomplete in certain details, since he was dealing with preserved material. Moreover, at the time when the specimens were sent to him I had not succeeded in recognising all the larval instars. Indeed I cannot even now be quite certain that I have correctly determined the number of the stadia. Dyar's law is inapplicable to a larva with no sclerotised parts and subject to a

considerable increase in size during any one stadium. The exuviae are so delicate that it is difficult to find more than traces of them. In the case of most of the ecdyses I have had the fortune to dissect hosts containing larvae that had begun to moult. This is not so, however, for the ecdysis between what I have assumed to be the third and fourth parasitic instars; there is therefore no positive evidence that these are not actually a single instar. Moreover, from the beginning of the third to the end of the fourth parasitic stadium there is comparatively little change in form in either sex. But in view of the great increase in size during this period it seems more probable that two stadia are comprised.

The following can therefore be added to Blair's original description.

The adult male (fig. 36 (Blair's fig. 1)).

Predominant colour in life a dull dark brown, the dorsum of the thorax almost black, scarcely shining; the eyes jet black, shining; the abdomen almost

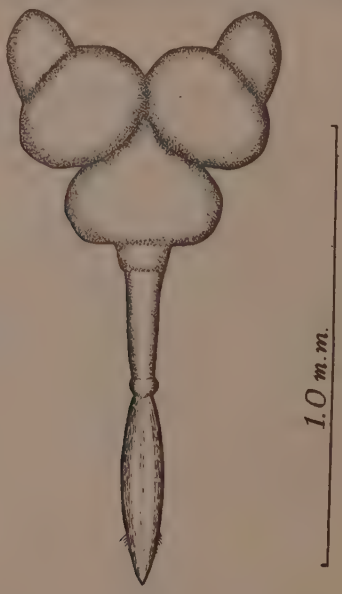

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Fig. 15.—*C. antestiae*. Reproductive organs of adult male.

black beneath, greyish-brown on the dorsum during life but darkening at death; the intersegmental membranes greyish. Last tarsal segment pale brown. Wings smoky brown, the veins almost black. Length of body, excluding the antennae and the deflexed last abdominal segment, about 4·0 mm. during life, sometimes rather more when the abdomen is fully distended. At death the abdomen shrinks rapidly and considerably. Antennae 0·95 mm. long, the maxilla together with the palp 0·43 mm. Expanse across wings 5·5 to 6·0 mm.

Genitalia (fig. 15) simple, the testes globular with a smaller accessory lobe,

opening without a vas deferens into an unpaired heart-shaped vesicula seminalis. Aedeagus lanceolate, brownish-yellow, 0·4 mm. long, with about six minute forwardly directed bristles on each side towards the apex.

The adult female (fig. 16).

Blair has stated that the cephalothorax of the adult female is asymmetrical. While this is quite correct, it should be pointed out that the asymmetry is an acquired character depending on which side of the host extrusion occurs. Just before extrusion the cephalothorax is quite symmetrical. The cephalothorax of the female figured by Blair (his fig. 3) is one which had been exserted on the left side of the host. The outer side (in respect of the position in the host), *i.e.* the right-hand side of this figure, is always more regular and less indented than the inner side.

Fig. 16.—*C. antestiae.* Adult female, unfertilised.

Perhaps the most remarkable thing about the female of *Corioxenos*, which so far as I know has no parallel in the animal kingdom, is the fact that it has two genital openings, one on each side of the cephalothorax, through either of which fertilisation can be effected. The females of other species of Strepsiptera, of which the hosts are for the most part Hymenoptera and Homoptera, have a single median genital opening, but then the cephalothorax is exserted from the host's abdomen in such a position that the opening is readily visible by and accessible to the male (*vide* Perkins' (1918) figure of *Stylops aterrima* Newport in the act of copulating).

The exserted cephalothorax of *Corioxenos* is, on the contrary, usually quite concealed by the wings of the host and it is clear that, if there were a median genital opening, it could only be reached with difficulty, if at all, by the aedeagus of the male. They " must," therefore, have two openings, one on each side,

since it is pure chance on which side of the host extrusion will take place. Speculation on how such an adaptation has arisen must be left to evolutionists.

The abdomen of the adult female, as of the later larval instars of both sexes, has eight * backwardly projecting dorsal prominences. The function of these is, I think, mainly to increase the absorptive area of the body surface, but they also serve as locomotor organs. By rhythmical movements of the prominences the larva is able to move slightly within the body of the host and in this way is no doubt able to get into the correct position for extrusion. In the fertilised female (fig. 17) the abdomen swells so much that the prominences disappear.

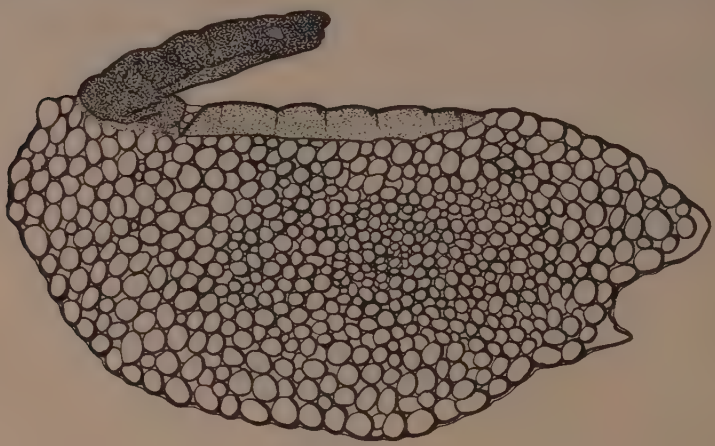

Fig. 17.—*C. antestiae.* Adult female, fertilised.

The first instar, or triungulin, larva (fig. 18).

In life the triungulin is shining black, from 0·25 to 0·27 mm. in length and about 0·10 mm. in breadth. The central pair of tail bristles is 0·11 mm. long; at 0·065 mm. from the base there is a swelling which is a reservoir for the sticky secretion from the glands in the apex of the abdomen (Cooper, 1937). The duct of this gland opens just beyond the reservoir; the terminal third of the bristles is exceedingly fine. The eyes are not readily visible in the living triungulin, but are easily seen in the nearly mature embryo (fig. 19). Having penetrated a host the triungulin swells considerably and the intersegmental membranes become visible. The method of ecdysis is described in Section 4.

The second (first parasitic) instar.

The first parasitic instar larva, shortly after it has left the exuviae of the triungulin, is somewhat scarabaeoid in shape, the anterior end being the stouter (fig. 20). When extended it is about 0·4 mm. in length, but it is usually slightly curved. Traces of the eyes of the previous free-living instar are just visible as a

* Blair's fig. 2, which shows only six dorsal prominences, is incorrect in this respect.

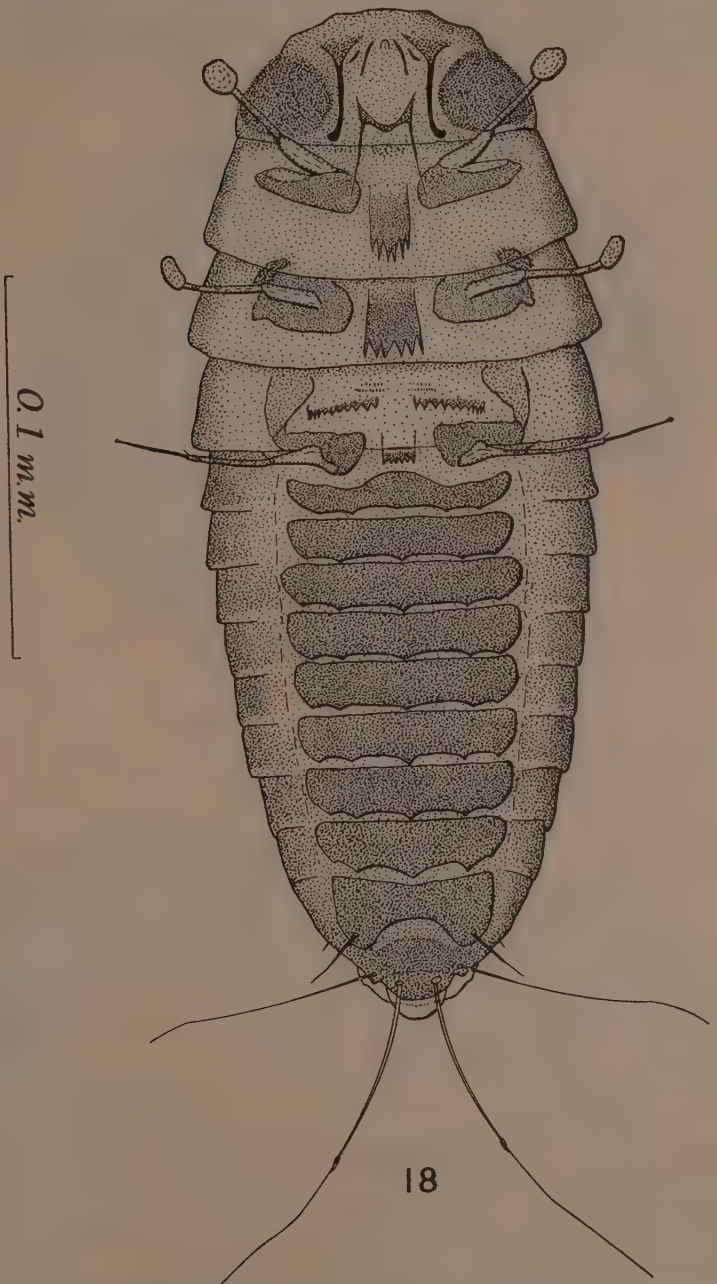

Fig. 18.—*C. antestiae.* Triungulin larva (ventral view).

pair of dark spots; three pairs of very inconspicuous protuberances represent all that remains of the legs of the triungulin. Segmentation is scarcely visible.

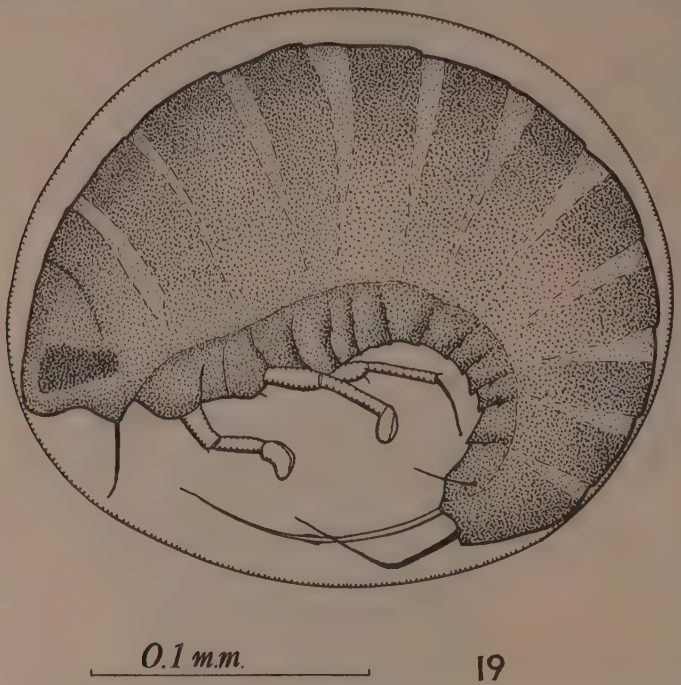

Fig. 19.—*C. antestiae*. Mature egg just before eclosion of triungulin.

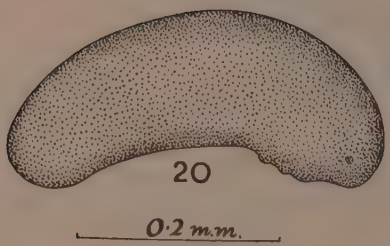

Fig. 20.—*C. antestiae*. First parasitic instar larva, at beginning of stadium.

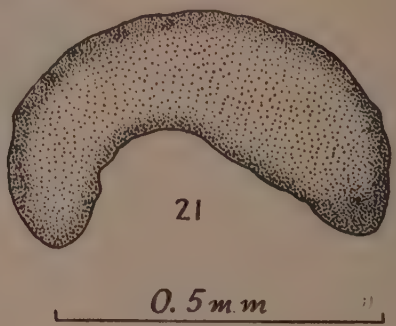

Fig. 21.—*C. antestiae*. First parasitic instar larva, at end of stadium.

Towards the end of the stadium (fig. 21) the size has increased to about 0·6 mm. and the eye-spots tend to disappear.

Shortly before ecdysis the larva, which in fact has already developed to the next instar, shrinks slightly and becomes completely detached from its old skin

before this is actually shed. This also occurs before each subsequent ecdysis, so that a larva of one instar may often be seen completely within the integument of the previous instar (fig. 28). I have been unable to distinguish between the sexes of the first parasitic instar larvae.

The third (second parasitic) instar.

In both sexes this is about 1·1 to 1·4 mm.* in length, the male (fig. 22) being thicker in proportion than the female (fig. 23) and as a rule less curved. Segmen-

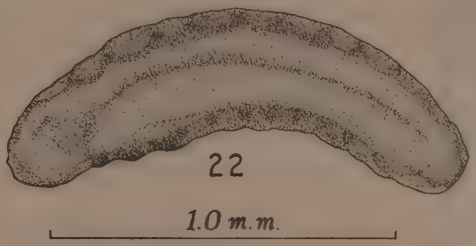

Fig. 22.—*C. antestiae.* Second parasitic instar larva, male.

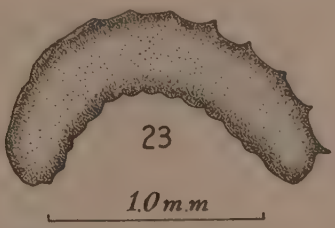

Fig. 23.—*C. antestiae.* Second parasitic instar larva, female.

tation, though still ill-defined, begins to be apparent. The male retains traces of the legs, but these are no longer seen in the female. In the female indications of the dorsal prominences are first visible. In the male these can, towards the end of the stadium, be detected under the skin, but they do not actually appear until the next instar.

The fourth (third parasitic) instar.

The male (fig. 24) is 2·7 to 2·8 mm. in length. The segments of the head, thorax and abdomen are now distinct and the leg rudiments are more conspicuous. Traces of the mouth-parts are just discernible. The female (fig. 25) is about the same length but more slender. The eight dorsal prominences are now well-marked.

The fifth (fourth parasitic) instar.

The male larva (fig. 26) is 3·6 to 3·7 mm. long, and the female (fig. 27) rather less. The dorsal prominences are now conspicuous in both sexes although

* These and subsequent measurements of the larvae are made from living specimens that were, so far as could be judged, at about the maximum size attained during the stadium.

those of the male are, as they are in later stages, much smaller than those of the female. Otherwise there is little apparent change from the previous instar.

Fig. 24.—*C. antestiae.* Third parasitic instar larva, male.

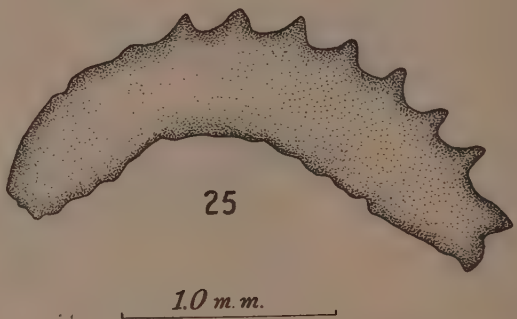

Fig. 25.—*C. antestiae.* Third parasitic instar larva, female.

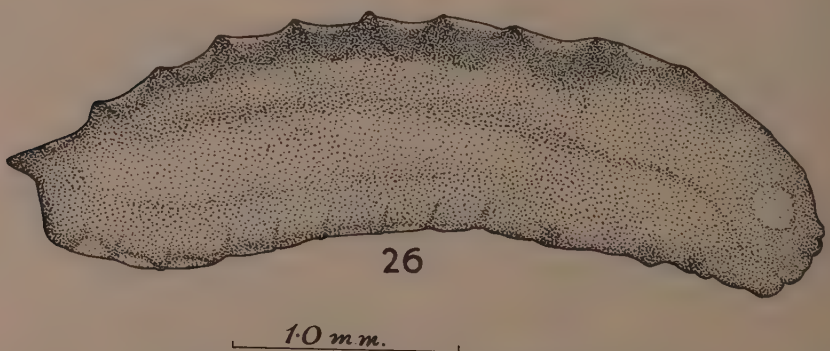

Fig. 26.—*C. antestiae.* Fourth parasitic instar larva, male.

The sixth (fifth parasitic) instar.

The male larva is about 4·0 mm. long. (Fig. 28 shows a male larva of this instar before it has shed the skin of the previous instar, and therefore before it

Fig. 27.—*C. antestiae.* Fourth parasitic instar larva, female.

Fig. 28.—*C. antestiae.* Fifth parasitic instar larva, male.

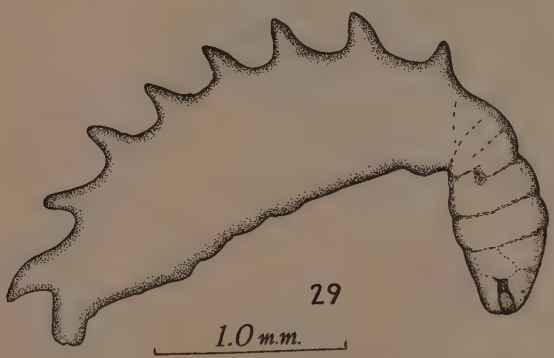

Fig. 29.—*C. antestiae.* Fifth parasitic instar larva, female.

Fig. 29*a*.—*C. antestiae.* Head of same.

has attained its normal size.) The spiracles, but not the mouth-parts nor any other part of the cephalothorax, are now sclerotised. The female larva (figs. 29, 29*a*) is about 3·3 mm. in length, *i.e.* very little larger than the previous instar. The spiracles and mouth-parts, but not the rest of the cephalothorax, are sclerotised. The cephalothorax is more or less permanently bent downwards almost at right angles.

The seventh (sixth parasitic) instar.

In the male (figs. 30, 30*a*, also Blair's fig. 5) the mouth-parts are sclerotised and there are sclerotised plates on the cephalothorax, which is ventrally

Fig. 30.—*C. antestiae.* Sixth parasitic instar larva, male before extrusion.

30*a*

Fig. 30*a*.—*C. antestiae.* Head of same, ventral view.

deflected more than in previous instars. At its maximum size the larva is about 5·0 mm. in length. During this stage extrusion takes place, after which the

cephalothorax becomes strongly sclerotised and dark brown in colour (figs. 31, 31*a*).

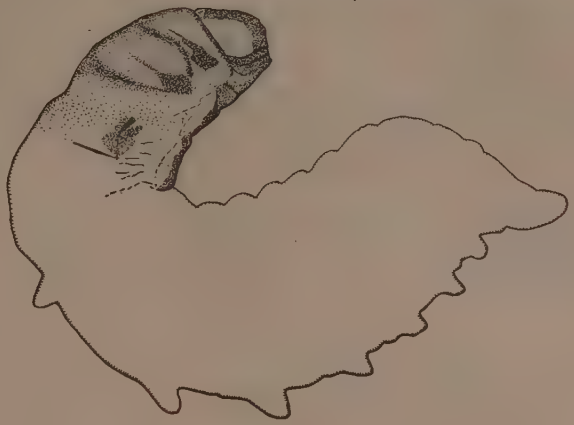

Fig. 31.—*C. antestiae.* Sixth parasitic instar, male, after extrusion.

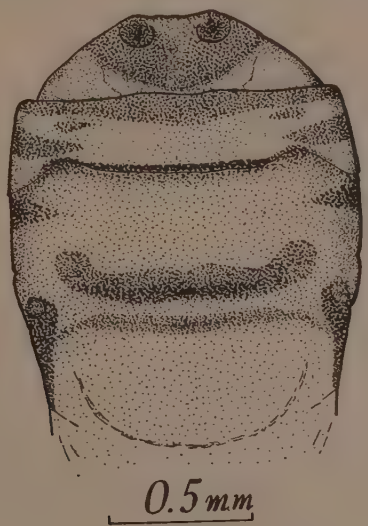

Fig. 31*a*.—*C. antestiae.* Cephalothorax of same, dorsal view.

The female larva of the sixth parasitic instar is about 3·6 mm. long. Before extrusion (fig. 32) the cephalothorax is slightly sclerotised and the " windows " (the pair of genital openings) become visible. After extrusion the cephalothorax becomes strongly sclerotised and chestnut brown in colour.

The eighth (pupal) instar of the male.

Soon after extrusion the male larva pupates within the skin of the last larval instar. The pupa is retracted from the exserted cephalothorax and is therefore entirely enclosed within the body of the host. The integument of the male pupa is very delicate. A few days before the adult male emerges the pupal integument is completely shed and pushed down to the posterior extremity of the last larval skin. The duration of the adult stadium is therefore in reality much longer than the two or three hours which are the span of its free active life.

There is nothing corresponding to a pupal instar in the female, the adult being formed within the close-fitting skin of the last larval instar. A female can be recognised as adult by the presence of the slightly sclerotised ventral abdominal band (fig. 16).

Fig. 32.—*C. antestiae.* Sixth parasitic instar larva, female, before extrusion.

(2) Outline of the Life-history.

In order to avoid frequent repetitions and explanations in the following pages, it seems convenient to begin with a brief outline of the life-history of this parasite, for although in general it resembles that of most other species of Strepsiptera, so far as any information is available about them, there are several important points that are here made known for the first time.

Except where another species is mentioned, "*Antestia*" or "the host" refers to *A. lineaticollis* Stål, the species on which the greater number of experiments and observations has been made. Information concerning the stylopisation of other species of *Antestia* is given in Part III, Section 9.

The term "triungulin" is used to describe the free-living, campodeiform first-instar larva. This term has been used by the majority of those who have written about Strepsiptera, and while it is true, as pointed out by Perkins (1905), that the free-living larvae of Strepsiptera lack the very feature—the three-clawed last tarsal segment—on which the word triungulin is founded, yet there

seems little to be gained by adopting the word " triungulinid " and still less by coining a new term, such as pseudo-triungulin or planidioid.

" Maternal host " or " parturient host " means an *Antestia* containing a female *Corioxenos* that has been fertilised and is producing triungulins.

" Potential host " means a nymph of *Antestia* spp. to which triungulins have attached themselves, but which has not yet been penetrated by them.

The triungulins emerge from the body of the female *Corioxenos*, escaping through the cephalothorax, and crawl about on the body of their maternal host, from which they become detached either by jumping from it or by coming in contact with some object.

Having left their maternal host they spend most of the time motionless, in an attitude well adapted for being picked up. At intervals they crawl short distances before resuming the same posture—referred to as " the waiting attitude." They are able to exist for at least a fortnight, under suitable conditions, without finding a potential host; they are quite remarkably resistant to adverse weather.

If picked up by any insect other than an immature *Antestia* they leave it again at the first opportunity. When, however, they become attached to a potential host they adopt a different posture, and it is then extremely difficult to dislodge them.

They do not immediately penetrate a potential host, but remain motionless on its exterior until its next ecdysis, when they are able to penetrate it.

When attached to a potential host they can remain alive for a very long time, 34 days being the maximum recorded with certainty, and it is only exceptionally that an *Antestia* fails to moult within a much shorter period than this. They can penetrate at any of the five ecdyses. Between two and five days after penetration the integument of the triungulin splits transversely between the head and thorax, and the first parasitic instar larva emerges into the body cavity of the host. There are probably six parasitic instars before the fully-grown (seventh parasitic instar) larva of either sex extrudes its cephalothorax from the body of the host. The parasitic instars feed on the blood of the host by diffusion through their skin. No direct damage is done to the organs of the host, such atrophy as occurs being literally atrophy, *i.e.* due to lack of nourishment consequent upon the presence of the parasite.

Extrusion of the cephalothorax, which cannot occur until the host has become adult, is invariably between the third and fourth abdominal tergites (*i.e.* between the *apparent* first and second tergites) (fig. 35). Only the actual cephalothorax is extruded, the whole of the abdomen including the sclerotised first segment which is united with the cephalothorax, remains within the body of the host.

Female larvae (with no exceptions) are extruded close to the pleura and male larvae (with very few exceptions) as near the middle as possible. The period of development, from entry of the triungulin to extrusion of the mature larva, is somewhat longer for a male than for a female. A male larva pupates very soon after extrusion, but the pupal stage is of comparatively long duration, so that the total period of development is over half as long again for a male as for a female. A female larva, without any intervening pupal stage, becomes adult and capable of being fertilised a few days after extrusion of the cephalothorax.

The males always emerge in the morning; they live a free active life of some two to three hours only, during which time they can copulate with as many females as time and opportunity allow.

The females never leave the host; copulation is effected by the male piercing with its aedeagus one of the "windows," situated on either side of the female's cephalothorax, which is on the outer side in relation to the host. Parthenogenesis never occurs. A female can be fertilised at any time during a period of about five to eight weeks. After this its ova degenerate and though copulation may take place, fertilisation does not follow. A single act of copulation, lasting perhaps a few seconds, is as efficient in procuring fertilisation as repeated acts either by the same male on one day, or by other males on following days.

The period of incubation, from fertilisation to the emergence of the triungulins from their maternal host, is usually between six and nine weeks, according to the temperature. A single fertilised female can produce over 3500 triungulins, during a period of about three months.

(3) The Free-living, or Triungulin, Larva.

(a) *Emergence.*

The triungulins emerge from the female either through the oral aperture, or through the opening, previously made by the aedeagus of the male, in the "window" on the outer side of the female. In many (possibly most) cases the hole thus made appears to be insufficiently large and the triungulins escape only through the oral aperture.

They emerge at any hour of the day and also during the night, though judging from individuals kept in the laboratory, rather more seem to appear during the afternoon, and rather fewer at night, than at other times.

Having got clear of their parent, they crawl about on their maternal host for a period which varies between a minute or two and several days. They become detached from the *Antestia* either by jumping from it or by coming into contact with any part of the coffee bush on which it is feeding, or with some other insect.

(b) *Locomotion.*

They move in short jerks, at the rate of about one mm. in thirty-five seconds in cool weather, but less slowly in warmer weather or if exposed to the sun. At a temperature of 25° C., in the laboratory, the average rate of progression (ten journeys by five different individuals) was one mm. in fifteen seconds, and it was much the same on a cool day but in full sunlight out of doors. Although most authors who have described the habits of the triungulins of other species of Strepsiptera have referred to them as "exceedingly active," this can scarcely be said to be true of the species considered here. One of the longest uninterrupted journeys recorded was of 4·2 mm. in 80 seconds. They do not as a rule continue moving for more than a minute or less at a time without stopping and adopting the "waiting attitude."

In this position, in which they spend most of the time until they either get picked up by a potential host, or die, the two anterior pairs of legs (of which the last tarsal segment is provided with an adhesive empodium) are held in the air, the front pair projecting forwards at an angle of 45°, and the middle pair at right angles to the body. This is raised at an angle of about 40° and is supported by the hind pair of legs and the central pair of tail bristles. The tarsi of the hind legs project forwards and the central tail bristles are doubled up under the body, the lateral pair of tail bristles being held in the air (fig. 33).

In order to adopt this position they grip with the two anterior pairs of legs, raise the abdomen high into the air, and bend the central tail bristles downwards and forwards under the abdomen, which is then lowered. Poised

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Fig. 33.—*C. antestiae.* Diagram of triungulin in "waiting attitude."

in this way they are perfectly adapted for fastening on to any moving object which encounters them. They frequently stay in this position for hours (if not days) at a time, either quite motionless or sometimes swaying a little from side to side, subsequently moving perhaps only a very short distance and then adopting the same attitude again.

(c) *Tropisms.*

The triungulins are positively phototropic, though not very definitely so. If numbers of them are placed on a sheet of paper in front of a window, nearly all will adopt the waiting attitude facing the light. Similarly the majority, but by no means all, tend to crawl towards a source of light. On the other hand, just as many seem to remain on the shaded side of a coffee berry as on the side exposed to the sun. They are neither positively nor negatively geotropic. They are definitely not stereotropic, except when they are attached to a potential host. It is obvious that if they were inclined to hide in crevices they would stand less chance of being picked up.

Numerous experiments to find out whether they were attracted towards the smell of a nymphal *Antestia* gave no positive results; this being so, it can only be said that it is unexplained how, having been picked up by an immature *Antestia*, they should "know" that they have found a potential host, and not allow themselves to be detached from it.

When they are in the waiting attitude the triungulins are able to jump a considerable distance, at least ten mm. vertically and nearly twenty-five mm. horizontally. The exact mechanism by which the jump is effected is not known, since it takes place much too quickly for any precise details to be observed. Probably the hind legs are the main source of propulsion, but the doubled-under tail bristles may also to some extent serve as a spring. Ability to jump has also been recorded for the triungulins of other species of Strepsiptera (Saunders, 1853).

They seldom, perhaps never, jump unless stimulated to do so by the near approach of some object, and it is only by objects of certain colours that any large proportion is attracted. Detailed evidence for this somewhat remarkable faculty for distinguishing colours has been given in a separate publication (Kirkpatrick, 1937).

It will suffice to say here that the attractive colours are red, black and orange. White, green and blue are comparatively non-attractive. Pure yellow is intermediate, but the addition of a little orange makes it definitely attractive.

Black and orange are the predominant colours of *Antestia*, so that it is probable that this faculty of colour vision enables rather more triungulins to find a potential host than would otherwise do so. But it must be admitted that so far as observations go, far more seem to become attached to an *Antestia* nymph through direct contact than by jumping on to it.

(d) *Transportation.*

When in the waiting attitude, and also, though a little less readily, when crawling, they will immediately attach themselves to any moving object, such as another insect, that happens to touch them. Should this object be anything except an immature *Antestia* they usually leave it at the first opportunity, which means that in most cases they get off again on to some part of the coffee bush at a greater or lesser distance, according to the activity of the insect to which they become temporarily attached, from where they were picked up. It will be clear from what has already been said about their slow and infrequent movements, that unless the triungulins should be transported they would not move far from the place where they became detached from their maternal host. A dead *Antestia* containing a parturient female was pinned on a leaf of a small coffee plant on which no other insects were present; after four days a few triungulins were found up to six inches away, but the great majority had moved two inches or less, and were still either on the same leaf or on the one immediately above or below it.

The list of insects to which I have observed triungulins to become attached comprises practically all those with which experiments have been made, and includes species of the orders Orthoptera, Hemiptera, Coleoptera, Hymenoptera and Diptera, and also (in the laboratory) the adult male of their own species.

From the majority of these, as has been said, they detach themselves at the first opportunity. I have, however, observed that large numbers picked up by a Hispid beetle were unable to free themselves from its spines. Doubtless there are other insects that, either from excessive hairiness or the presence of a secretion, prove fatal to the triungulins.

It is probable that they sometimes get attached to aerial insects that are on the point of leaving the coffee bush, and thus get deposited in a place where they would have no chance of finding a host.

This habit the triungulins have of utilising other insects as vectors is perhaps scarcely to be considered as a genuine case of phoresy * since, though of frequent occurrence, it is purely fortuitous. The habit must, however, inevitably result in the wider distribution of the triungulins and in the

* Phoresy is a term proposed by Lesne (1896) for the phenomenon of one animal apparently deliberately and for its own benefit utilising another as a vehicle of transportation. Lesne's typical example was a saprophagous Borborid fly, which rides on the back of a dung-beetle and oviposits in the ball of dung that the beetle constructs. Most other examples of genuine phoresy are concerned with parasites, such as certain Scelionid egg-parasites of Orthoptera, of which the adult attaches itself to the female host on which it remains until the host oviposits, when it lays its own eggs in the egg-mass of the host. (Chopard (1922), quoted by Imms (1931).)

One of the most extraordinary instances is the case of *Dermatobia hominis* Say—the "human bot-fly." This fly is said to haunt the breeding-places of mosquitos, capture the adult mosquitos as they emerge, and lay its eggs upon them. When the mosquito begins to feed upon a man the eggs (which already contain mature first-instar larvae) hatch, presumably owing to the warmth imparted, and penetrate the skin. (Curran, 1934.)

The procedure adopted by *Corioxenos* is much less remarkable and more haphazard than the above, but it is of too frequent occurrence to be dismissed as mere accidental transportation.

survival of a greater number of individuals than if they were only distributed by their maternal hosts. The following experiment gives an indication, though under highly artificial conditions, of the efficacy of the distribution of the triungulins by another insect. A fifth-instar nymph (of which the prevailing colours are black and orange) of a species of *Nezara* was confined for one hour in a small cage containing a coffee berry on which were 25 triungulins. It was then transferred to another cage containing two third-instar *Antestia* nymphs and left there for 18 hours before removal. In one of these hosts seven *Corioxenos* developed and in the other three.

The readiness of the triungulins to attach themselves to any object and then to transfer to another has proved of great assistance in experimenting with a known number of triungulins to each potential host. It is a simple matter to pick up a triungulin on the point of a needle and then to touch any part of an *Antestia* nymph, to which, in nine cases out of ten, it will adhere immediately.

(e) *Survival and mortality before finding a potential host.*

If the opportunity offers, a triungulin will attach itself to a nymphal *Antestia* immediately after issuing from its parent, and should that *Antestia* be on the point of moulting, it is able to burrow in at once. If, however, no potential host is immediately available, the triungulins are capable of surviving a surprisingly long time. It is probably impossible to ascertain how long this time is under normal conditions on a coffee bush. In one experiment a dead parturient host was fixed to a leaf of a small potted coffee plant, fully exposed to the sun and rain, at 09h. on 4.xii.35. Living triungulins were found on the plant up to 09h. on 10.xii.35, though none after 16h. on that day. During this period of six days the mornings were mainly sunny, and a total of 25·3 mm. of rain fell, including one shower of 13·4 mm. in 30 minutes.

In another similar experiment a dead parturient host was attached to a small exposed coffee plant on 14.xii.35 and removed on the morning of 18.xii.35. In the afternoon of that day a nymphal *Antestia* was allowed to walk about on the plant for five minutes. It was observed to have picked up a number of triungulins, five of which subsequently penetrated and developed. On 18.xii, 3·4 mm. of rain fell in 8 minutes; and on 19.xii, 9·6 mm., of which, so far as could be judged from the chart of the recording rain-gauge, 6 mm. fell in less than five minutes. A few triungulins were still present on 20.xii, though on the following day none could be found. In experiments in which triungulins were placed in the middle of a large sheet of blotting-paper fastened on a board and fully exposed to sun and rain, some have been found alive after 73 hours, but the majority were washed off the paper by heavy rain and may not necessarily have been killed.

Experiments under artificial conditions indicate that they are capable of surviving for much longer periods than might be inferred from the foregoing.

(*a*) At a relative humidity maintained constant at 86% (the average maximum temperature during the period being 26° and the average minimum 20·2°), nearly all survived for 15 days and some for 19 days. This is the longest recorded time for which they have survived without finding a host, though I have many records (Table 12) of their having lived for much longer periods externally on a host, when a delayed

ecdysis on the part of the latter has postponed their chance of penetrating it.

(*b*) In a cardboard box in the laboratory, the relative humidity uncontrolled (varying from about 70% to 90%), the average maximum temperature being 24·5° and the average minimum 21·5°, some survived for 15 days.

(*c*) At a relative humidity of 100%, two out of twenty-five lived for twelve days, but the others had previously become entangled in the hyphae of a fungus, and died.

(*d*) At a constant relative humidity of 30%, most survived 84 hours but all were dead in 96 hours.

(*e*) About 25% of those kept at a constant relative humidity of 10% lived for 72 hours, but all were dead in 80 hours.

(*f*) Kept in a refrigerator at an almost constant temperature of 4·5°, all survived for 48 hours, and started moving within ten minutes of being taken out. The same ones were put back into an almost constant temperature of 0° for a further 30 hours, after which about 70% of them had died, but the remainder recovered.

Their resistance to high temperatures for short periods was tested by placing numbers of triungulins on a piece of blotting-paper enclosed in a small glass tube immersed in a water bath. A thermometer inserted through the cork of the tube presumably gave a close indication of the temperature to which the triungulins were subjected.

(*g*) Subjected for ten minutes to a temperature of 49·0° rising to 49·5° at the end of the period, after four minutes all were exceedingly active; after seven minutes nearly all had ceased moving, and at the end of the ten minutes all were inactive, lying flat on the paper, *i.e.* not in the usual waiting attitude. One hour after being restored to the normal room temperature of about 25° all were still lying motionless and flat. Three hours after, one or two showed signs of movement, and on being picked up on the point of a needle, fourteen were found to be alive and attached themselves readily to an *Antestia*; the remaining eighteen were apparently dead. Of these fourteen, five (at least) were observed to enter the *Antestia* at its fourth ecdysis, which took place on the following day, and four of these completed their development.

(*h*) Ten triungulins were subjected to a temperature of 43·0°, rising at the end of the period to 45°. The majority moved actively for thirteen minutes, being in fact much more active than at normal temperatures, and never remained in the waiting attitude for more than a few seconds at a time. After seventeen minutes all had become motionless and were lying flat. They were then removed. Some showed signs of life two minutes later, and after two hours all seemed to be alive and attached themselves to a host. The host moulted four days later and it was subsequently found that seven out of the ten had penetrated and developed.

Their powers of resistance to complete immersion in water are quite extraordinary, as the following experiments show:—

(*i*) Eight triungulins were immersed in distilled water for four hours, then exposed to the noon-day sun for one hour, after which they were put on a fourth-instar nymph. The nymph moulted three days later;

six out of the eight penetrated and developed, five (three males and two females) arriving at maturity.

In the following six experiments (*j*–*o*) a large number of triungulins (which incidentally had emerged from a female in a host that had died four days previously) were immersed in distilled water for seventeen hours; they were then dried in the sun from 08h.30 to 10h.30 on 13.xi.35. Very nearly all of them survived this treatment and they were then placed on six fourth-instar nymphs, ten being put on each nymph, with the following results :—

(*j*) Two days to next ecdysis of host. Four penetrated and developed, of which all (three males and one female) arrived at maturity.

(*k*) Nine days to next ecdysis of host. Four penetrated and developed, of which all (two males and two females) arrived at maturity.

(*l*) One day to next ecdysis of host. Seven penetrated and developed, of which two females arrived at maturity, but the host died prematurely, since it also contained four fully grown male larvae and one female larva.

(*m*) Two days to next ecdysis of host. Six penetrated and developed, of which three females became adult and two males and one female failed to become exserted.

(*n*) One day to next ecdysis of host. Seven penetrated and developed but the host died before any became adult; it contained five sixth-instar male larvae and two fully grown female larvae.

(*o*) Two days to next ecdysis of host. Three penetrated and developed, all three (two males and one female) becoming adult.

Thus of the 60 triungulins which in these experiments were put on to six potential hosts 31 entered and developed, a proportion comparable to that successful in developing under normal laboratory conditions (Table 12).

(*p*) Ten triungulins were immersed in 1% NaCl solution for 72 hours. On being dried in the sun, nine of them were found to be still alive. These readily attached themselves to a nymph, but none of them succeeded in penetrating at the next ecdysis (to the fifth instar) which took place ten days later.

(*q*) After 96 hours immersion in 1% NaCl solution, no triungulin out of a large number survived. Most of them had swollen so that the intersegmental membrane had become visible, and they appeared as if they were on the point of moulting to the first parasitic instar, though none of them did so.

Since it was suggested to me that spraying with Bordeaux mixture, which on many estates is carried out as a routine practice against *Hemileia* and leaf-fall, might be injurious to the triungulins, the following experiment was made :—

(*r*) Twenty triungulins were immersed for fifteen seconds in a Bordeaux mixture nearly twice as strong as that normally employed, and then left for an hour to dry. They were then all alive and ten were put on each of two fourth-instar *Antestia*, which moulted eleven and fourteen days later. Five larvae developed in each host, producing three adult males, four extruded females and three females unable to extrude.

The foregoing experiments are at least sufficient to show that the triungulins are not likely to be destroyed in large numbers by any ordinary weather conditions. Moreover, even if prolonged wet weather may at times be responsible for some mortality among them, it must be remembered that a parturient female, provided that its host survives, is capable of producing young over a period of at least three months, so that the proportion of her total brood destroyed by weather conditions could at most be small.

The triungulins are, however, readily caught and killed by any sticky substance. In a small cage, many are entrapped in the excreta of *Antestia*, and (though this has not been verified by observation) I should expect that on a bush on which Coccids or Aphids were numerous large numbers would become stuck in the honey-dew.

Triungulins are able to emerge from a female contained in a dead host for at least seven days after its death, provided of course that the conditions are such that the body of the host remains moist. Under field conditions it is probable that it would dry up in a much shorter time. Such triungulins have just as much vitality and power of survival as those that have emerged from a living host. It has also been proved that triungulins emerging from females contained in *Antestia* that were moribund, or had actually died, as a result of arsenical bait spray (Part I, Sections 7, 8) were quite healthy and capable of survival.

No predators on the triungulins have been observed, and, though this is not to say that none exists, it seems unlikely that any predacious species would be sufficiently attracted by such a small and tough insect to cause appreciable mortality.

It therefore seems probable that the chances of the survival of a triungulin depend almost entirely on its finding a host—or rather on a host finding it—within a period of, say, about ten days.

(f) *Attachment to potential hosts.*

If an *Antestia* nymph walks over any surface on which triungulins are present in large numbers, it picks them up in a manner that reminds one of a carpet-sweeper. Most of the triungulins adhere in the first place to the legs, a few to the antennae, and some to the ventral surface of the abdomen. The *Antestia* usually tries to remove them from its antennae, though they then frequently adhere to the front legs, used for dislodging them.

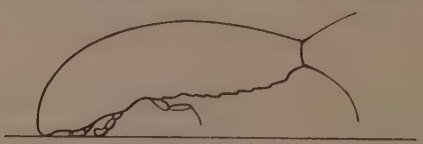

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Fig. 34.—*C. antestiae*. Diagram of triungulin in the attitude adopted when on a potential host.

Having got on to a young *Antestia*, the triungulins crawl about until they have found a suitable spot from which they cannot be, or at least are unlikely to be, removed. The most usual places are almost anywhere on the dorsum of the thorax or abdomen, on the sternum between the coxae, or between the head and thorax. When once they have settled down they seldom, if ever, move again until the next ecdysis of the host, they never adopt the

waiting attitude, and it is difficult to dislodge them without injuring them. Their position (fig. 34) is, in fact, the exact opposite of the waiting attitude. They grip the potential host with the two front pairs of legs and also, it appears, take some sort of hold with their mouth-parts, since if they are pushed from the side with the point of a needle they can be pivoted round on their heads without being dislodged. The abdomen is held in a convex position, the hind legs and the tail bristles being raised above the surface of the *Antestia*.

That they do occasionally leave a potential host, though whether voluntarily or not cannot be said, is suggested by the fact that on a few occasions, in experiments where a known number of triungulins were placed on each nymph of several kept together in the same cage, some of the individual hosts have developed more parasites than the number of triungulins placed on them. This may possibly be explained by the fact that triungulins sometimes get left behind on the exuviae of a nymph that has moulted, and may then transfer themselves to another nymph.

The triungulins are able to penetrate an *Antestia* at any of the five ecdyses, including the final one to the adult instar, but not on its eclosion from the egg, although to all appearances the first-instar nymph immediately after hatching is as pale and soft as a recently moulted one. Several experiments have been made in which triungulins were put on or near batches of eggs on the point of hatching, and though many attached themselves to the newly hatched nymphs, none attempted to penetrate.

The triungulins undoubtedly leave, or get detached from, nymphs of the first instar more readily than those of later stages; consequently the proportion of triungulins that attach themselves to nymphs of the first instar and successfully penetrate at the first ecdysis, is rather lower than the proportion that penetrate at any of the succeeding ecdyses except the final one (Table 12). In an experiment in which four triungulins were put on to each of twelve first-instar nymphs, twenty-five penetrated and developed. Of these five for certain, and probably three others, did not penetrate until the second ecdysis. It is, moreover, unlikely that second-instar nymphs often become stylopised in the field, for during the first stadium *Antestia* nymphs are practically immobile, seldom moving far from their empty egg-shells, and taking little or no food. Consequently they would not as a rule meet with triungulins unless a host containing a parturient female, or a "vector" insect should chance to walk into a cluster of newly-hatched nymphs.

They do not search for a host with any semblance of "purpose": a nymphal *Antestia* may pass within a millimetre or less of a triungulin and the latter, unless it jumps on to the *Antestia*, will show no sign of recognition. But a triungulin actually touched by a nymph will adhere immediately.

(g) *The method of penetrating a host.*

As has been said, when a triungulin gets attached to an immature *Antestia* it quickly settles down and remains motionless until the next ecdysis of the host.

The act of penetration into the host has been watched on numerous occasions. As soon as the host starts to shed its skin, the triungulins present become exceedingly active, whatever the time of day or night, and regardless of temperature. They do not, however, appear to have much sense of direction, and have even been observed to walk back from the body of the new instar

nymph, which is their objective, on to the almost completely shed exuviae, on which they have been left behind. When they succeed in getting on to the soft pale body of the newly moulted host, they usually start burrowing into it within a few minutes. As a rule they bore in obliquely, though sometimes they have been observed to do so almost vertically. From the time they begin to penetrate until they are completely out of sight is usually about fifteen minutes.

They have been observed to penetrate almost any part of the host. The pronotum is the most usual place, but possibly only because this is where the majority of triungulins find themselves when they have left the partly shed exuviae. Or it may be (if there is any truth in the hypothesis that it is the moulting fluid which stimulates them to activity and penetration) because the glands secreting the moulting fluid are more numerous on the pronotum than elsewhere. That this is so in *Antestia* has not been verified, but it is said to be the case in the majority of insects (Comstock, 1925). Other places at which they have been observed to penetrate are the cervicum, any part of the thoracic sterna, particularly close to the coxae, and (much less frequently) the abdomen, either dorsal or ventral surfaces. They have on several occasions been seen to penetrate, in hosts that had just moulted to adult, the scutellum and corium. Thence, if they are to reach the body cavity and survive, they must go right through and burrow again through the tergum. I have no evidence that they ever succeed in doing this, and I know that in a few of the instances where a triungulin entered the scutellum, it failed to penetrate further.

It will be seen from Table 12 that the proportion of triungulins that succeed in developing when they have become attached to a fifth-instar nymph, and should therefore penetrate at the final moult, is smaller than the proportion that are successful at the four previous ecdyses. At least part of the difference may be accounted for by those which, in attempting to penetrate the newly moulted adult, enter the scutellum or corium and are unable to progress further.

If triungulins do not start penetration within about 20–30 minutes from the beginning of ecdysis they seem unable to accomplish it. I have several times observed triungulins to get on to a newly moulted host but fail to penetrate, although many of them remained alive until the host's next ecdysis, when they succeeded in penetrating. Such cases are, however, comparatively uncommon, the majority of those recorded being of triungulins that became attached to a first-instar nymph, and succeeded in getting on to the second instar but did not penetrate until the second ecdysis. At the subsequent ecdyses nearly all the triungulins that leave the exuviae and attach themselves to the new instar are successful in boring into it.

I am still uncertain what the stimulus is which, when the host starts moulting, urges the triungulin to activity, although it has been completely motionless for the whole time since it became attached. It might possibly be a chemical stimulus provided by the "moulting fluid." Yet at the time of ecdysis the moulting fluid appears to have been almost completely absorbed, and the skin of the new instar to be quite dry, as it is, according to Wigglesworth (1933), with most insects.

Moreover, several experiments were made in which a clean needle was rubbed on an *Antestia* in the act of moulting and then brought into close proximity with triungulins immobile on the back of another nymphal host, but no response was ever evoked. Neither were active triungulins, crawling

about on a piece of paper, attracted to a part of the paper that had been rubbed with a moulting nymph. The negative result of these experiments is, of course, not conclusive, and the suggestion that the moulting fluid is the stimulus may perhaps be supported by the fact that triungulins will not penetrate first-instar *Antestia*, although on eclosion from the egg they are just as soft as they are after an ecdysis. The curious fact (discussed in Part III, Section 5) that triungulins seldom penetrate hosts with malformed antennae may also possibly be explained by such hosts being deficient in the glands secreting the moulting fluid. I have also noticed that triungulins very rarely attempt to enter a host that dies shortly after an ecdysis, because it could not completely free itself from the exuviae. On the other hand, the triungulins are, under certain circumstances which are discussed below, occasionally capable of entering an *Antestia* long after it has become adult, when there could be no question of the moulting fluid acting as a stimulus.

(h) *Survival and mortality when attached externally to a potential host.*

Apart from the not very frequent instances, mentioned previously, in which a triungulin attaches itself to the new instar after ecdysis, but fails to penetrate, the time for which it must survive externally on the host, if it is to develop further, depends on the period elapsing between its finding a host and the next ecdysis of the latter. The maximum period is therefore determined by the duration of the various stadia of *Antestia*. Tables 1–5 (in Part I) summarise all the information I have been able to collect on the duration of the five stadia, under laboratory conditions, with abundant food and under different conditions of temperature.

Temperature has a very large effect on the duration of the stadia, at least on the average duration, but I have several records of an individual bug, hatched from the same batch of eggs as others which have developed in normal time, and kept under identical conditions, being much slower than the average in developing. It is, however, a comparatively rare occurrence for a stadium to last so long that all the attached triungulins have died before the next ecdysis.

Table 12 * shows, for a total of 6764 triungulins put on to 1000 *Antestia* kept in the laboratory, the proportion that survived until the next ecdysis and then succeeded in penetrating and developing, in relation to the number of days it was necessary for them to remain externally on their potential host; and in relation to the particular ecdysis of the host at which they entered. The number placed on each nymph varied between one and fifteen, but was usually five or seven, less often ten. I have already explained how simple a matter it is to pick up a triungulin on the point of a needle and transfer it to a potential host. The nymphs were kept separately, each in a small cylinder of celluloid, resting on blotting-paper and covered with a glass plate. All were fed on full-sized but still green coffee berries.

Of the total of 6764 triungulins placed on these 1000 potential hosts, 3446 or 51% succeeded in developing.

It will be seen from the right-hand column of each section of the table that there is, as was to be expected, a progressive decrease in the number of survivors according to the time elapsing between the triungulins becoming attached and their entry into the host at its next ecdysis. This decrease is, however, very small for the first nine days, and even if the triungulins have to remain externally

* Nymphs with malformed antennae (Part III, Section 5) are not included in this table.

Table 12.

Survival rates of triungulins of *Corioxenos*.

No. of days from attachment of triungulins to next ecdysis of potential host	Next Instar of Potential Host																					Total (all instars)				
	Adult					Fifth					Fourth					Third					Second					
	No. of potential hosts	No. that failed to become stylopised	Total no. of triungulins attached	Total no. of triungulins that penetrated and developed	% of triungulins successful in developing	No. of potential hosts	No. that failed to become stylopised	Total no. of triungulins attached	Total no. of triungulins that penetrated and developed	% of triungulins successful in developing	No. of potential hosts	No. that failed to become stylopised	Total no. of triungulins attached	Total no. of triungulins that penetrated and developed	% of triungulins successful in developing	No. of potential hosts	No. that failed to become stylopised	Total no. of triungulins attached	Total no. of triungulins that penetrated and developed	% of triungulins successful in developing	No. of potential hosts	No. that failed to become stylopised	Total no. of triungulins attached	Total no. of triungulins that penetrated and developed	% of triungulins successful in developing	No. of potential hosts	No. that failed to become stylopised	Total no. of triungulins attached	Total no. of triungulins that penetrated and developed	% of triungulins successful in developing
1–3	21	3	171	63	36·8	84	2	659	376	57·0	115	2	652	437	67·0	25	0	135	98	72·6	14	2	55	28	50·9	259	9	1672	1002	59·9
4–6	33	4	266	98	36·8	57	1	397	236	59·5	99	2	599	401	67·0	20	0	108	71	65·7	12	1	33	17	51·5	221	8	1403	823	58·7
7–9	26	3	212	66	31·2	50	1	327	194	58·7	59	1	345	213	61·7	20	0	130	76	58·5	6	1	25	7	28·0	161	6	1039	556	53·5
10–12	35	3	255	81	31·7	45	1	320	154	47·5	40	1	254	148	58·3	10	0	63	32	50·8	1	0	1	1		131	5	893	416	46·6
13–15	30	5	268	86	32·0	42	1	316	153	47·9	34	1	214	119	55·6	4	0	29	15	51·7	—	—	—	—	—	110	7	827	373	45·1
16–20	27	0	279	84	30·0	28	2	218	99	45·4	14	1	72	28	38·9	8	1	46	20	43·5	—	—	—	—	—	77	4	615	231	41·3
21–25	15	6	149	16	10·7	6	1	45	13	28·9	2	1	10	2	—	2	1	5	2	—	—	—	—	—	—	25	9	209	33	15·8
26–30	4	1	28	6	21·4	2	1	12	2	—	1	0	4	2	—	—	—	—	—	—	—	—	—	—	—	7	2	44	10	22·7
31–35	1	1	5	0	—	1	1	5	0	—	5	3	43	2	—	—	—	—	—	—	—	—	—	—	—	7	5	53	2	3·8
36–40	—	—	—	—	—	—	—	—	—	—	2	2	9	0	—	—	—	—	—	—	—	—	—	—	—	2	2	9	0	0·0
Total	192	26	1633	500	30·6	315	11	2299	1227	52·8	371	14	2202	1352	61·4	89	2	516	314	60·8	33	4	114	53	47·3	1000	57	6764	3446	51·0

on a potential host for as long as twenty days, the proportion surviving is still over 40%, or about 80% of the average survival. After 20 days the mortality appears to increase considerably, but the number of potential hosts that fail to moult within this time is naturally small. The longest time for which triungulins have been known to survive externally on a potential host, and then to succeed in developing, is 34 days in two instances, in one of which one out of fifteen, and in the other one out of five, survived for this length of time. Many have survived for more than 19 days, which is the longest time they have been known to exist in the absence of a potential host.

Since the triungulins do not feed, whether they have found a potential host or not, it is probable that their ability to survive longer when on an *Antestia* is due to decreased metabolism consequent upon cessation of activity.

The ecdysis of the host at which the triungulins enter has a distinct bearing on the proportion that are able to develop. Of those due to penetrate at the second or third ecdysis, *i.e.* entering the third or fourth-instar nymph, the survival rate is over 60%. Why it is distinctly less, under 53%, when they are due to enter at the fourth ecdysis, is unexplained. It was to be expected that rather fewer (47·3%) would survive when placed on first-instar nymphs, since they are known to become detached from these more readily than from the later stages. I do not, however, fully understand why the survival rate of those that were placed on fifth-instar nymphs, and therefore ought to have penetrated when the host became adult, should be as low as 30·6%. To some extent this is accounted for by the fact that some of the triungulins enter the scutellum and the corium of a host that has just moulted to the adult instar, and I believe that these fail to penetrate to the body cavity. But I do not think that a sufficient number do this to account for such a large reduction in the survival rate. It will also be observed from Table 12 that of 192 potential hosts of the fifth instar, 26, or nearly 14%, failed to become stylopised at all. On the assumption that all potential hosts are equally liable to be stylopised, this proportion is far in excess of the mathematical expectation, whereas of 775 hosts of the fourth, third and second instars, only 27 failed to become stylopised, a number only about twice as great as the theoretical probability.

There is therefore little doubt that for some unexplained reason attachment to a fifth-instar nymph gives a triungulin a poorer chance of survival than does attachment to an earlier instar.

Under field conditions the proportion of triungulins that succeed in finding a potential host is naturally a very small fraction of what it is under the sheltered and confined conditions of cages in an insectary. To maintain the species in stable equilibrium it is only necessary for about two of the progeny of each female, or, say, 0·2%, to survive to maturity. (The fact that one male is capable of fertilising several females, and therefore that it is not necessary for an average of one male from each parent to survive, is probably roughly balanced by the cases in which a female fails to become fertilised and by those in which the host dies before the female parasites it contains have produced triungulins.)

At what stage the enormous mortality of the triungulins occurs can only be conjectured, but I think that it is almost entirely due to failure to find a host, and that of those which are successful in finding a host the proportion of survivors is likely to be almost as large in the field as in the laboratory.

Antestia nymphs with triungulins attached externally have been exposed to heavy rain and hot sunshine without any effect on the triungulins, a normal proportion of which have penetrated at the next ecdysis. Fifteen nymphs of the third and fourth instars were enclosed in a wire gauze cage on a part of a

coffee bush, together with one adult *Antestia* containing one parturient female *Corioxenos*. This was left for seven days and then removed; after all the nymphs had undergone an ecdysis these were also removed and kept singly in the laboratory until they died. (Those containing eight or more parasites died prematurely.) They were found to contain the following numbers of parasites: 16, 16, 15, 12, 11, 11, 10, 10, 9, 8, 5, 5, 4, 4, 2, or a total of 138. Assuming that during the seven days for which the parturient host was on the tree it gave birth to 90 triungulins per day (a rate slightly higher than the maximum recorded in the laboratory), then 22% of the 630 produced were picked up, penetrated and developed. This large percentage is, of course, accounted for by the fact that the parturient host and the fifteen nymphs were confined together in a comparatively small space. The wire gauze used for the cage was of the widest mesh that would prevent the escape of the nymphs, and could not have afforded any considerable protection. During the period that they were on the tree (31.x.–15.xi.35) 19 mm. of rain fell, including one shower of 6 mm. at the approximate rate of 1 mm. per minute, and there was bright sunshine on the majority of the mornings.

In another experiment ten triungulins were placed on each of ten fourth-instar nymphs, which were then liberated on a small isolated coffee bush, completely unprotected in any way, on 4.v.36 and left there until 23.v.36. At the end of this period, during which a total of 250 mm. of rain fell, only four out of the ten *Antestia* were recovered. In one of these six *Corioxenos* developed, in two of them five each; the remaining one had not moulted, but a single triungulin was still alive on it externally. This was transferred to a fresh nymph which moulted two days later. It successfully penetrated and eventually became an adult male.

I have frequently watched triungulins in the act of penetrating an *Antestia* and even when the number was large, twenty or more, the host never showed any signs of discomfort.

The number of triungulins that will, given the opportunity, penetrate a host is governed only by the number that can find room to attach themselves. Several experiments were made in which nymphs were allowed to crawl about on coffee berries covered with large numbers of triungulins, until they could apparently pick up no more, and as many as sixty-six have been known to penetrate and develop—though, of course, not to maturity, since from such excessive multiple parasitism the host always dies prematurely (Part III, Section 4).

Much larger numbers of triungulins have been recorded entering an adult *Antestia* that already contained a parturient female, and developing at least to the first or second parasitic instar, as is described below.

Providing that triungulins successfully accomplish their first ecdysis, instances of subsequent premature mortality are exceedingly rare. Except when the presence of too many parasites in one host renders the extrusion of some of them impossible, I have only two or three times found dead larvae of any of the parasitic instars within a living host. There is, however, a small premature mortality (about 2%) of males that have become adult, but for some reason have been unable to free themselves completely from the pupal exuviae.

(i) *Entry into adult* Antestia.

I have shown that the normal time of entry of the triungulins into a host is immediately after an ecdysis, whether to the second, third, fourth, fifth or adult

instar. They have never been known to try to penetrate a nymph except at the time of ecdysis.

They are, however, able to enter, and develop in, an adult *Antestia* that contains extruded *Corioxenos* of either sex. Over 300 have been known to penetrate a host containing a parturient female and also the pupa-case of an emerged male. When this host died, a few of these had attained the third parasitic instar, though most were in the first and second. In addition there was a large number of unmoulted triungulins in the body cavity.

They are also able to penetrate a host that contains only a non-parturient female or a male, though comparatively few do so, since, as the host is not itself producing triungulins, it is only those it may chance to pick up that have the opportunity of entering. They appear to enter where the intersegmental membrane is broken at the point of extrusion of the mature parasite. This habit of penetrating a mature stylopised adult occurs under field conditions, but probably to a much smaller extent than when the hosts are kept in small breeding cages in the laboratory. Especially when no immature *Antestia* are present the emerging triungulins can find no suitable hosts and are constantly attaching and re-attaching themselves to the adults present.

Having penetrated into an adult *Antestia* through the intersegmental membrane, they develop normally, though I have no record of their doing so beyond the male pupal stage. But there seems to be no reason why with only one or two mature parasites of the original infestation, and only one or two triungulins subsequently entering, a host should not bring a second generation, as it were, to maturity. This phenomenon is exceedingly rare among insects parasitic on insects, though according to Imms (1931) a parallel has been recorded by Timberlake experimenting with the Braconid *Dinocampus coccinellae* Schr. (*americanus* Riley), which is parasitic on COCCINELLIDAE.

However, any large number of triungulins entering and developing within an already stylopised host entails, at least under laboratory conditions, the premature death of the host. In the laboratory certainly, and probably also in the field, this second-generation parasitism is disadvantageous to the parasite, for it tends to produce premature mortality among hosts containing parturient females.

Very exceptionally triungulins are able to penetrate an unstylopised adult *Antestia* and to develop within it. The place where they enter is not known; probably it is through the intersegmental membranes of the abdominal tergites. Out of over fifty adult *Antestia*, known to be unstylopised, and enclosed with very large numbers of triungulins (so many that some of the *Antestia* must at times have had more than one hundred triungulins on them) only two became stylopised, one containing four larvae and the other one. Possibility of error (*i.e.* that triungulins might have been accidentally attached to the *Antestia* before they became adult, and have entered in the normal manner at an ecdysis) was precluded by the fact that the larvae (one male and four females) were alive when the hosts were dissected. If they had penetrated even at the final ecdysis they would have become adult long before.

(4) The Parasitic Larva.

After penetrating a host the triungulins do not immediately moult, as other species of Strepsiptera are said to do (Pierce, 1909). At least up to 36 hours after penetration they are unchanged in appearance and, if dissected from their host, still active. Between two and three days after having penetrated

they swell considerably and the intersegmental membranes of the abdomen become readily visible, as they are in embryos shortly before hatching (fig. 19).

(a) *The first parasitic stadium.*

The first ecdysis takes place about three days after entry (when the average temperature is about 23° C.). This period is prolonged to at least six days in cooler weather (19°–20° C.). The great majority of triungulins that have succeeded in entering a host are also successful in undergoing the first ecdysis. Occasionally, however, a dead unmoulted triungulin has been found within the body cavity.

It will, of course, be readily understood that such information as is given on the intermediate stages of *Corioxenos* has been obtained by the examination of hosts that have been killed, or have died, a known number of days after the entry of the triungulin. Since the time of entry is in every case known to within a day, and since some 200 stylopised *Antestia* have been examined with the sole view of tracing the development of the parasite, the estimated times for the duration of the several stadia are unlikely to be seriously in error.

On several occasions I have dissected, in Ringer's solution, a host when a contained triungulin was on the point of undergoing ecdysis. The head splits dorsally from the prothorax but remains hinged on the ventral side; the thoracic and abdominal segments do not split, though the intersegmental membranes of the latter are greatly distended—as they have been for about a day previous to the ecdysis. The first parasitic instar larva then wriggles its way out of the exuviae; the process from the time the head-capsule has become semi-detached until the larva is free takes about five to ten minutes. For some little time after the larva has got clear it continues wriggling actively.

It is a little difficult to be certain when larvae that have undergone the first moult in the thorax, as most of them do, migrate to the abdomen of their host. I think that in any case they do not do so early in the first parasitic stadium, since the few very young larvae that may be found in the abdomen can probably be accounted for by the (comparatively) few triungulins that directly penetrate the abdomen. Larvae that have nearly completed the first parasitic stadium are also not infrequently found in the thoracic cavity but, at least when a host contains only a small number of parasites, only seldom are larvae of the second parasitic instar to be found there. It is therefore presumed that the migration normally, though possibly with many exceptions, takes place towards the end of the first stadium. If, however, there are a very large number of *Corioxenos* in one host, those larvae that are unable to find room in the abdomen are quite capable of developing in the thorax, on rare occasions even up to the point when they should normally be exserted through the tergum of the abdomen. But it is probable that such larvae originally moved into the abdomen during their first stadium and were subsequently pushed back into the thoracic cavity by force of competition.

(b) *The later parasitic stadia.*

The precise method of ecdysis of the later instars is somewhat uncertain but, judging from the few larvae that I have been fortunate enough to find in the act, the old skin, which for some time previously has become completely detached from the new instar larva (fig. 28), is ruptured transversely towards the anterior end. The larva then wriggles out from the old skin of the abdomen as from a bag. Male larvae that have just moulted to the sixth parasitic instar have been

found completely free of the abdominal exuviae but with the exuviae of the head still adhering.

Before extrusion of the cephalothorax the young larvae are to be found in any position in the abdomen of the host and occasionally, as already stated, in the thoracic cavity. Their head may be pointed to either end of the host, less commonly they lie transversely. All the parasitic instars can make slight movements, which, in the later stages, appear to be facilitated by the dorsal prominences.

The earlier instars, at least, almost certainly feed entirely by diffusion * through the skin. Larvae of the later instars can be seen to make frequent movements with their rudimentary mouth-parts, but whether these play any part in nourishment is uncertain. I have failed to keep larvae, removed from their host, alive in nutrient solutions.

(c) *Duration of the stadia.*

The approximate average duration of the stadia during the warmer season (December to March) at Amani, when the temperature in the laboratory ranged from a maximum of 24° – 26° C. to a minimum of 20° – 22° C. is shown in Table 13.

TABLE 13.

Duration of the parasitic stadia of *Corioxenos.*

Number of days after entry of triungulins until ecdysis to	Males	Females
2nd (1st parasitic) instar	3 (*a*)	3 (*a*)
3rd (2nd parasitic) instar	10–12	10–12
4th (3rd parasitic) instar	16–20	15–17
5th (4th parasitic) instar	24–26	20–22
6th (5th parasitic) instar	28–30	24–26
7th (6th parasitic) instar	30–32	27–28
Extrusion of seventh instar from host (*b*)	33–35	28–32
Pupa	40–44	—
Adult	52–55 (*c*)	34–36 (*d*)

Notes :—

(*a*) Possibly slightly less, but known to be more than 60 hours.

(*b*) That is, supposing that the host has by this time become adult. If it has not, extrusion is of necessity delayed. In such cases of enforced delay extrusion can probably take place immediately the host moults to the adult instar, and certainly within 36 hours of its doing so.

(*c*) The shortest time actually recorded, under the conditions stated, was 50 days.

(*d*) Judged by when the female is capable of being fertilised by a male. The shortest time actually recorded, in a single instance only, was 31 days.

(d) *Extrusion of the cephalothorax.*

The cephalothorax of both sexes is invariably extruded through the intersegmental membrane between the third and fourth † abdominal tergites (fig. 35).

* The term osmosis, which has frequently been used for this method of alimentation, is incorrect.

† *I.e.* as stated by Blair (1936), between the apparent first and second tergites. The first tergite is a very small and easily overlooked sclerite, and the second and third are more or less fused together.

No exception to this rule has been found in over 2500 stylopised hosts examined. The mature larva lies ventral side upwards within the body of the host, the extruded cephalothorax is bent backwards and lies in close apposition to the dorsum of the host's abdomen, its dorsal side is therefore uppermost.

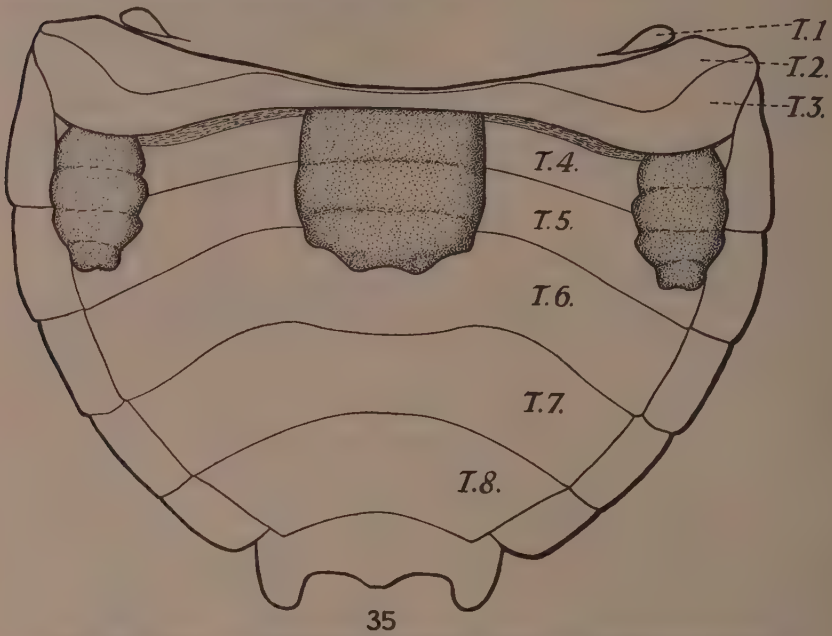

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Fig. 35.—Diagram of the abdomen of *Antestia*, showing the position of extruded *Corioxenos* (one male and two females).

Without exception the females are extruded close to the pleura of the host. In the few instances in which a third female has become extruded in one host it has sometimes been found to overlap one of the others, and sometimes to lie parallel, but nevertheless as close to the side as possible.

The cephalothorax of the male is almost always extruded as near the middle as possible, even when the host contains no females, which would have pre-occupied the outside positions. Occasionally, where two males are present, one (probably the first to be extruded) is in the exact centre, and the other then necessarily somewhat to one side. Where there are three or more, one or two of them may occupy a place as near the pleuron as that usually occupied by a female, though sometimes, in their endeavour to avoid the side positions, two or more of them may overlap.

It is clear that the instinct of the female to choose the side positions is essential for the survival of the species; if they did not they could never be fertilised. It appears less necessary for the male to choose the centre, though the fact that it does so ensures that a female that may have entered at a later ecdysis of the host will still find a place for extrusion, even though one or two males, having entered at an earlier ecdysis, are already extruded. The number and sexes of the extruded *Corioxenos* contained in 2000 hosts are given in Tables 19 and 20 (Section 8).

(5) The Adult Male.

(a) *Emergence from the pupa.*

The males emerge from the pupae during the morning, always between one and a half and seven hours after sunrise, and the great majority between two and four hours after. They tend to emerge earlier on bright sunny mornings than on dull days; similarly emergences were found to take place at an earlier hour on a verandah facing the east, and in a greenhouse exposed to the morning sun, than in the laboratory. It also appears (though I have not sufficient data to say that it is proved) that emergence can be delayed for at least one, and possibly two or even three days, if the mornings are heavily overcast. I have repeatedly observed that during a succession of two or three sunless mornings very few males emerge. But on the first bright morning many will appear, the triungulins of which had penetrated their hosts (kept under identical conditions) during a period stretching over at least three days. However, the length of time from the entry of a triungulin to the emergence of an adult may (as is discussed below) occasionally vary by as much as four or five days in the same host, so that it would need a very large number of observations to prove whether or not emergence is delayed by dull weather. No instance has been recorded of a male emerging later than 13h. 30 (and only a single and possibly doubtful case of one emerging after 12h. 45), even when a dull morning has been followed by a sunny afternoon. This appears somewhat remarkable, seeing that it is almost certain that the stimulus that causes the male to emerge must be light, even though the amount of light penetrating under the scutellum of an *Antestia* cannot be large. Not only do the facts already related tend to show that light is the necessary stimulus, but I made an experiment in which five hosts, known to be likely to produce adult males within a few days, were kept in complete darkness from 06h. 30 until 19h. 00, and from 19h. 00 until 06h. 30 were illuminated by electric light. All the six males produced by these hosts emerged between 21h. 30 and 24h. 00. (As they were not watched all night, it is just possible that some may have emerged after midnight, but since they were all quite dead by 06h. 30 on the following day, they could not have emerged much later.)

In the apparatus used for the foregoing experiment the temperature rose a few degrees when the light was turned on in the evening. Normally, of course, there is also a rise in temperature after sunrise, it might therefore be thought that it was the rise in temperature, rather than light, which stimulated emergence.

Seeing however that (1) emergences—even though comparatively few—have been observed on dull mornings when there has been no rise in temperature; (2) they were, as a rule, slightly earlier on a verandah facing the east than in a room facing west, although the temperature was higher in the latter than in the former; (3) in a greenhouse exposed to the morning sun, in which the morning rise in temperature was both large (7°–10° C.) and rapid, the males tended to emerge only a little earlier than on the cool but equally bright east-facing verandah, it seems probable that a rise in temperature is not the necessary stimulus.

A few males have been observed to emerge successfully from a host that had died on the preceding day. I extracted one from its pupal integument, contained in a host that had just died. It survived for 24 hours and was then found to be fully active and capable of fertilising several females.

During the ten to fifteen minutes before the male actually gets free from its

host, the latter usually becomes agitated, walking rapidly a short distance, and then stopping to fan its wings as if preparatory to flight. The process of emergence takes as a rule some minutes, and the head and thorax of the partly freed male can be seen, during one of the periodical wing-movements of the host, appearing from under the tip of the scutellum. As has been explained, the pupa lies ventral side uppermost within the abdomen of the host, so that the male, emerging through the bent-over cephalothorax of its larval skin, comes out with its feet on the dorsum of the abdomen and facing the posterior end of the host.

When the male is nearly free, the *Antestia* frequently assists the process by pushing it out with its posterior legs; though the treatment thus given often appears to be rough, I have never observed that a male has been injured by it.

If there are more males than one in a host sometimes they all emerge almost together at intervals of not more than five minutes, or there may be an interval of an hour or slightly more; while not infrequently they emerge on different days.

Table 14 shows, for a total of 200 *Antestia* bred individually in the laboratory, from which two or more male *Corioxenos* emerged, the number of days, if any, elapsing between the emergences.

Expressed in a different manner, when two or more males emerged from one host (having entered it together, at the same ecdysis) in 39% of the cases they emerged on the same day; in 27% emergences were spread over two days; in 15% over three days; in 10·5% over four days; in 5% over five days; in 3% over six days, and in 0·5% over seven days.

The table does not include four instances from which it was clear from the number of days (13–18) elapsing between emergences, that the triungulins had

TABLE 14.

The number of days, if any, elapsing between the emergence of two or more male *Corioxenos* contained in the same host.

Two males	Three males	Four males	Five males
xx (64)	xxx (12)	xxxx (1)	xxxxx (1)
x1x (39)	x1xx (7) xx1x (7)	xxx1x (1)	
x2x (17)	x1x1x (4) x2xx (3) xx2x (3)	xxx2x (1) xx1x1x (1) x1xx1x (1)	
x3x (17)	x1x2x (2) x2x1x (2)		
x4x (7)	x1x3x (1)	xxx4x (1) x1x1x2x (1)	
x5x (4)	x4x1x (1) x5xx (1)		
	x1x5x (1)		

x indicates the emergence of a male.
The figure, if any, between two x's is the interval in days between emergences.
The figure in brackets is the number of instances recorded.

entered at different ecdyses of the host. For it is quite possible for a host to produce two males, the triungulins of which had penetrated at different ecdyses, in which case (conditions of temperature being equal) they emerge at an interval approximating to the interval between the two ecdyses. And though it has not been observed, there is no reason to suppose that a host could not produce three or even four males, which, as triungulins, had penetrated one each at the second, third, fourth and fifth ecdyses of the host.

As soon as a host is rid of its emerging male parasite it usually becomes calm and often starts feeding at once.

The male is capable of flight and copulation immediately after getting clear of its host. I have in fact more than once watched a male that did not leave the *Antestia* from which it emerged, but at once started copulating with a female *Corioxenos* in the same host.

(b) *Flight.*

The method of flight of male Strepsiptera has often been described as a series of rapid darts (Pierce, 1909). I suspect that this is because they have chiefly been observed in a small cage, in which case the above description is also true of this species. But if they are in the open, they fly quite steadily and slowly, with the body held almost vertically. This method of flight has been recorded by Muir (1906) observing *Elenchoides perkinsi* Pierce (*Elenchus tenuicornis* Muir *nec* Kirby).

If let loose in a room they tend to fly upwards, though they often come down again. As a rule they fly towards a source of light, but their positive phototropism is not very well-marked.

It is difficult to follow their movements when they are flying about among coffee bushes, and I have almost immediately lost sight of most of those I have watched, but they appear to hover among the branches in a manner reminiscent of Pipunculid flies. If confined in a small space, however, between the rapid darting flights of short duration, they walk about the bottom or sides of the cage, though even when walking the wings are kept in almost constant motion. At times, especially perhaps when about to pounce on the back of an *Antestia*, they make a distinct buzzing sound, how produced I have been unable to discover. When flying steadily in the open they are quite silent. Pierce (1909) has recorded that *Xenos* (*Acroschismus*) *pallidus* Brues buzzes during the whole of its active life, and that the noise is made by the elytra. This is almost certainly not so with *Corioxenos*, which appears, at least while copulating and I think also when flying, to keep its elytra practically motionless, and held nearly vertically upwards.

The active life of the male lasts only for two to three hours. Usually after about two hours they are incapable of copulating, and after at most three hours incapable of sustained flight. I have, however, observed one male that repeatedly copulated with two females in one host during a period of three hours and a quarter. It was then offered another stylopised *Antestia*, and immediately mounted it and penetrated the contained female which it successfully fertilised. At three hours and twenty-five minutes after emergence this male, though still active, would not copulate again. The foregoing appears, however, to be quite exceptional, and as a rule about three hours after emergence they are at most capable of a slow dragging walk in which the antennae and aedeagus are used to aid their now feeble legs. Although when confined in a cage they will show traces of life, by a slight twitching of the legs, up to six or seven hours after emergence, in the field they presumably never live for long after they have lost the power of

flight. If they are denied access to a female they live no longer than when they have spent the whole of their active life in intermittent copulation.

In a small cage, owing to their erratic and apparently aimless method of flight, they very easily become entangled in any moisture, such as the excreta of *Antestia*, that may be present. Having once got their wings wet, they are incapable of either further flight or of copulating. Judging, however, from their mode of flight in the open, it is probable that the premature mortality from such causes is actually much less than one would be led to expect from observations of the numbers that get thus entangled in a cage. I have been unable to observe what happens to an adult male during a shower of rain.

Natural enemies of the adult males are probably of little importance. Doubtless predaceous insects may account for a few, but the only observation made is of a single individual found caught in a spider's web.

(c) *Copulation.*

Exactly how the male is attracted to the female for the purpose of copulation is a question of considerable interest and is at present unsolved. Muir (1906) observing *Elenchoides perkinsi* arrived at the conclusion that sight was the sense by which the male found the female. To some extent my own observations confirm this, but it must be remembered that the female *Corioxenos* is usually entirely concealed, for as a rule it is only when there are also two or more males in the same host (and by the time these are exserted the females present may very likely already have been fertilised) that a female is so much pushed towards the side that it is partly visible. If therefore the male is attracted by sight, it is attracted to the host, and not to the female of its own species. This possibility is supported by the fact that a male will mount on the back of an *Antestia* that is not stylopised. Although it usually gets off again within a second or two, I have often seen one remain as long as a minute on an unstylopised *Antestia*, clinging on to the scutellum and tapping with its extended aedeagus all round the edges of the hemi-elytra, and also—though less frequently—other parts of the *Antestia* such as the head, prothorax and apices of the wings. I have also observed them to mount, though never for more than a few seconds, immature *Antestia* (which never have exserted females) and even other species of PENTATOMIDAE, and on one occasion a Cassidid beetle.

In some experiments made with a view to observing the exact method of copulation, I amputated the wings of a number of stylopised *Antestia*, so as to expose the extruded female parasites. When the wings on both sides were removed, copulation never took place; although a large number of males was introduced to *Antestia* thus treated, none mounted for more than a few seconds. When, however, *Antestia* were chosen that only had one extruded female, and the wings on the other side were left intact, copulation was observed in a few instances, though many of the males introduced would not perform the act. I suggest that this may be an indication that an unusual appearance of the host inhibits sexual attraction. On the other hand, males will copulate readily with females contained in *Antestia faceta*, which to us has a general appearance distinct from that of *lineaticollis*. They will not, however, copulate with females contained in *Antestia trivialis*, which in colour and general appearance is entirely different from *lineaticollis*. (See also Part III, Section 9.)

An experiment intended to ascertain whether the antennae of the male played any part in its search for a female was unsuccessful; it is obviously impossible to amputate the antennae of such an active insect without lightly anaesthetising it, and none so treated recovered properly from any anaesthetic

used, whether their antennae were amputated or not. (For the same reason it was not possible to experiment with males of which the eyes had been covered with an opaque substance.)

I think, however, that the sense of smell cannot play an important part in the search for a female, in view of the fact that a male quickly found, and mounted for a few seconds, an *Antestia* that had been soaked for five minutes in ether, and—at least to my olfactory sense—retained none of the typical Pentatomid smell. No males ever actually copulated with females contained in *Antestia* thus treated, which is perhaps hardly surprising, although I have often seen males copulate with females—probably still living—contained in hosts that had recently died.

Also, for what it is worth, it may be mentioned that males, enclosed in an empty box one half of the blotting-paper bottom of which had been rubbed over with squashed *Antestia*, were not noticeably attracted to that half.

I have several times dissected a live female *Corioxenos* (though how long it remained alive is difficult to say) from its host, covered its abdomen (which being moist would be liable to entangle the wings of the male) with a thin dry membrane and then offered it to a male. Copulation never took place with females extracted from their host, nor did any male show the slightest interest in them.

If the foregoing observations are correctly interpreted, *i.e.* if the sense of smell does not help the male to find a female, it is difficult to suggest what the function of the elaborate antennae of Strepsiptera may be. During the search for a female and during copulation the three branches of the antennae seem to be held wider apart than at other times, but they are not apparently brought into contact with the host.

Males, confined only with unstylopised *Antestia*, will sometimes mount them repeatedly during the whole of their active life. (I have recorded three cases in which a male was put with an *Antestia* which it was thought might contain a female *Corioxenos*, apparent penetration of the male's aedeagus under the wing of the *Antestia* was observed, yet on subsequent examination no parasite, of either sex, was found.) At other times I have observed that after one or a few preliminary investigations a male will take no further interest, and occasionally, even from the first, it will take no notice whatever of an unstylopised *Antestia*.

A male, which had previously been proved to be sexually potent, was enclosed in a small box with an *Antestia* containing two females, both of which were adult, and kept for two hours in complete darkness. It failed to fertilise either of the females.

It appears therefore that the male is attracted in the first place by sight, but to the host, not to its own female; having found a host it finds the female of its own species by touch—*i.e.* by tapping with its aedeagus. Should this be correct, and no other explanation appears to fit the repeatedly observed facts, it is difficult even to speculate on the manner in which such an instinct has been evolved.

The actual method of copulation is as follows. When a male finds an *Antestia* containing an extruded adult female, it mounts on its back—usually approaching it from behind—and grasps with its feet the thorax and scutellum. Sometimes it makes one or more circular movements, tapping all the while the sides and even the head and abdomen of the *Antestia* with its extended aedeagus—as they frequently do when they have found an unstylopised *Antestia*. Often, however, penetration of the female is effected

almost immediately, within perhaps one second of the male having mou[illegible]. The position adopted during copulation is shown in fig. 36.*

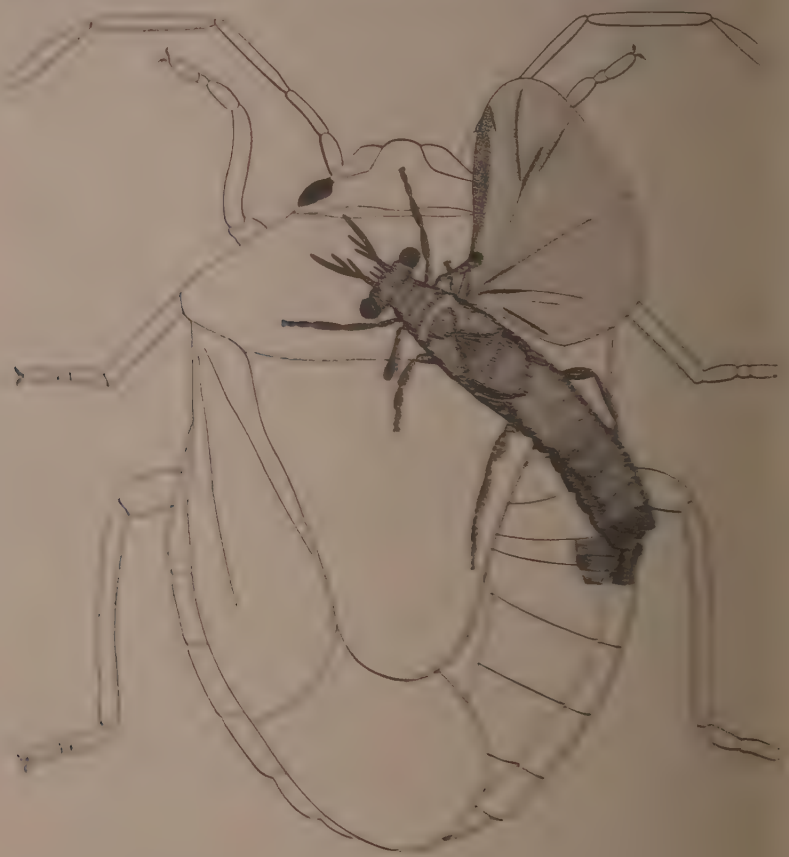


Fig. 36.

dislodge the male by pushing it off with their posterior legs. It is remarkable that, although I have watched the process of copulation several hundred times, I have never once seen a host attempt to get rid of the male by the simple expedient of fanning its wings. Sometimes, especially perhaps when the female is a virgin and the "window" has to be pierced, the male makes several jabs with its aedeagus before securing penetration. But often penetration, even of virgins, is obtained at the first attempt. The duration of copulation is from a few seconds to upwards of a minute. On two or three occasions I have seen a male, apparently unable to free itself, remain *in copula* for nearly five minutes.

If the male is confined with a single host containing a female, it usually dismounts after copulation for a period varying between fifteen seconds and two minutes or more, subsequently mounting and copulating again at regular intervals during the whole of its active life. If there are two females in the one host, the male will frequently copulate with both before dismounting.

The number of females that one male is capable of fertilising can only be guessed at, but is probably large. The most that I have recorded is 12, each of which was allowed access to the male for about two minutes, and all of which subsequently produced triungulins. Having fertilised these, it was still quite active, but no more females were available. Another male fertilised ten females in ten minutes, but was then unfortunately allowed to escape. There seems to be no reason why a single male should not be capable of fertilising a large number of females, provided, of course, that the concentration of hosts containing them is so dense that the male is able to find them during the course of its active life. On the other hand, I have several times observed a male that, although active and in no way damaged, appeared to be impotent and to take no notice at all of *Antestia* containing adult female parasites. Yet the testes of one of these apparently impotent males were full of active spermatozoa.

There appears to be no correlation between the duration of copulation and the number of triungulins produced. When penetration was deliberately interrupted after 5, 10 and 15 seconds, the female produced apparently as many young as when the male was allowed access to the female for the whole of its life. Similarly a female penetrated by a male eight times, but never for more than two seconds at each time, was completely fertile. Nor do three or four copulations (naturally by different males) at intervals of about seven to ten days appear to increase the number of young produced. The largest number of triungulins actually counted, produced by a single female, was 3720 spread over a period of 95 days (Table 15) and this was also the result of a single fertilisation.

Males will apparently copulate with females of any age—except during the first few days after they have become exserted, when they are still immature (Section 6 (b)). One male was observed to penetrate a female that had originally been fertilised some four months before, had been producing triungulins for two months, and of which the host died of old age a week later.

(6) The Adult Female.

(a) *Extrusion.*

Under normal laboratory conditions during the warm season at Amani, the female larva extrudes its cephalothorax about 28–30 days after it has,

as a triungulin, entered its host. That is, of course, assuming that the host has itself become adult by this time, for in no circumstances do *Corioxenos* of either sex become exserted from an immature *Antestia*. If the triungulin has entered at the first or second ecdysis, or if, as sometimes happens, the later stadia of the host should be prolonged for more than the normal period, the last-instar larva is quite capable of remaining alive, entirely concealed within the host's abdomen, until the final ecdysis enables it to extrude its cephalothorax. Even with triungulins that have penetrated at the first ecdysis, such enforced delay before extrusion is not usually (*i.e.* apart from delayed development of the host) more than about fifteen days, and it is known, from instances in which the development of the host has been delayed, that the larvae are able to remain alive for at least twice the normal period without becoming extruded.

It seldom happens (see also Tables 19, 20) that more than two females in one host can become extruded. When, however, several female larvae are present, those that fail to extrude not infrequently develop to the adult instar. It is not known accurately how long such totally enclosed adult females remain alive, but those which have (probably) been adult for a month or more always appear to be dead, and their gut is congested with opaque excremental matter.

Out of 1000 hosts bred separately in the laboratory 185 contained more than two adult female *Corioxenos*. One hundred and sixty-four of these had two extruded females and from one to six adult but unextruded. In only 21 was a third female extruded. The extrusion of four females has never been recorded.

When two females do succeed in becoming extruded on one side of the host their cephalothoraxes may either overlap, or, more often, they lie parallel. Two instances were recorded in which both the females on one side were fertilised; in one of these the second female was, when the host was examined, lying on the inner side of the other. It is, however, hardly possible that it could have been reached by the aedeagus of the male when in this position, so presumably it was overlapping the other female when it was fertilised, and subsequently became pushed to the inside position.

It is also possible for females to become adult, and males to develop to the pupal instar, entirely within the body of an immature *Antestia*. I have only seldom recorded this, but it is of sufficient interest to give one instance in detail. Five triungulins were put on to a third-instar *Antestia* on 3.iii.36. The host moulted to the fourth instar on 6.iii, and to the fifth on 19.iii. It died without having become adult on 25.iv, *i.e.*, it had remained in the fifth stadium for 37 days, or at least 23 days longer than the normal period at that time of the year. On dissection it was found to contain two male pupae, one adult female (which was in the thoracic cavity), and one fully developed female larva. The females were still alive when the hosts were dissected, though no sign of life could be seen in the male pupae.

(b) *Fertilisation.*

After extrusion of its cephalothorax a period elapses before the female has become adult and is capable of being fertilised. As the only means of ascertaining the length of this period is by introducing a male, if one is available, every day to a female that has recently become exserted, and noting whether it copulated, and if so was successful in fertilising the female, I have been unable to collect many data on this question. The shortest period recorded (once only) between the entry of a triungulin and the fertilisation of the female it produced, is 31 days. I have also one record of 32, one of 33, and several of 34

days. A male had been introduced to each of these females on the previous day and, though it had mounted the host and apparently shown considerable interest, it had not actually copulated. Since 27 days is the shortest time recorded for the period from the entry of the triungulin to the extrusion of the female larva, it appears that a female is adult and capable of being fertilised four days after it has extruded its cephalothorax, though about seven days is probably more usual.

The period for which a female remains capable of being fertilised is surprisingly long. One female to which no male had access until 119 days after it had, as a triungulin, entered its host, was then successfully fertilised. This was in the cool season, when development is slower, but since females in other hosts kept under the same conditions at the same time of the year were fertilised within 46 days from the time of their entry, it appears that the period during which a female can be fertilised may extend to some ten weeks. Copulation has frequently been observed with much older females, but has not resulted in fertilisation, apparently on account of the eggs having degenerated.

It may be remarked that Perkins (1918), observing *Stylops wilkellae* Perkins, thought that the females were only attractive to the males for a very short period, and that if they were not fertilised during this period they reproduced parthenogenetically, but this is certainly not true of *Corioxenos*.

Copulation nearly always appears to succeed in fertilising a female of suitable age; I have recorded only a few fertilised females that failed to produce triungulins—provided of course that the host lived long enough—and in most of these the fungus *Penicillium* sp. had gained access through the empty puparium of a male and had also attacked the female. (Part III, Section 6.)

I have found no indication that parthenogenesis ever occurs, but have amassed a considerable amount of evidence to show that it does not. Over 200 hosts containing only female *Corioxenos* have been kept singly until they died, no male parasite allowed access to them. None of these produced triungulins and, at least in females that had been adult for three months or more, the eggs appeared to have degenerated.

The proportion of females that succeed in becoming fertilised under field conditions is probably very large. Unfortunately in the earlier field counts (Part III, Section 7, Table 30) I neglected to distinguish between fertilised and unfertilised females.

In the counts made from December 1935 onwards, I recorded the percentage of females that were either parturient or contained well-developed eggs. It varied between 55% and 74% with an average of 67·5%. Many of the remainder would certainly have been recently fertilised, but time did not allow the examination of large numbers sufficiently closely to see if the " window " on the outer side of the cephalothorax had been pierced. I estimate that all those fertilised less than three weeks before capture were therefore not included and that the percentage actually fertilised would not have been less than 80.

Since the developmental period of the female is much shorter than that of the male (Table 13) a female is, under field conditions, likely to have already been fertilised before a male contained in the same host has emerged. As all the *Corioxenos* in one host would often, though not of necessity, be siblings, interbreeding is thus to a large extent avoided. Whether this is of any importance in the economy of the species is not known; in any case, females have, in the laboratory, been successfully fertilised by males bred in the same host, and known to have had the same parents.

(c) *Incubation period of the eggs.*

The period of incubation, from the time of fertilisation to the emergence of the first triungulins, is about six weeks during the warm season at Amani, and considerably more during the cooler time of the year (Section 7). The egg stage therefore lasts longer than all the subsequent developmental stages of the female and nearly as long as those of the male. Apart from insects that have a diapause in the egg stage (a phenomenon, so far as I know, rare among tropical insects) such a division of the developmental period is very unusual. It is presumably accounted for by the advanced state of development attained by the triungulins at the time of eclosion.

(d) *Production of triungulins.*

The period during which a fertilised female continues to produce triungulins is apparently determined only by the length of life of the host. Of 150 parturient female *Corioxenos*, the hosts of which were kept separately under observation in the laboratory, the only ones that ceased to produce triungulins before the death of the host were a few attacked by the fungus *Penicillium* sp. The host of these all died within a few days of the cessation of the production of triungulins.

The longest time for which a female *Corioxenos*, under laboratory conditions, has been known to produce triungulins is 95 days, and by good fortune this was one of the few of which the daily production of triungulins was accurately counted (Table 15). This female had only been fertilised once. Though I have often allowed males to fertilise the same female several times at intervals of a few days, it cannot be said whether this might result in an extended period of fecundity, since none of the hosts of these females lived as long as 95 days after first producing triungulins. There are no indications that more than one fertilisation increases the rate at which triungulins are produced.

I have found no trace of a spermatheca in the female. Several females, dissected at varying intervals up to about 14 days (in one instance 17) after they had been fertilised, had free active spermatozoa, usually in enormous numbers, in the body cavity. But in none of the females examined more than 18 days after copulation could I find a single live spermatozoon. It therefore seems certain that fertilisation of the eggs must be accomplished within at most

TABLE 15.

The average number of triungulins produced daily by five individual female *Corioxenos*.

	1st week	2nd week	3rd week	4th week	5th week	6th week	7th week	8th week	9th week	10th week	11th week	12th week	13th week	14th week	After death of host	Actual total
1	25	60	57	55	52	34	34	host died on 49th day.							not counted	2220
2	36	63	61	38	26	19	(2 days) 20	host died on 44th day.							60	1800
3	33	87	48	42	26	33	35	27	42	51	35	30	16	(4 days) 14 host died on 95th day	134	3720
4	12	29	(4 days) 50	host died on 18th day.											90	570
5	8	29	(6 days) 43	host died on 20th day.											198	715

about 17 days after copulation, yet it is known that the embryos may arrive at maturity over a period of 13 weeks. The eggs on the periphery are known to be the first to mature, a possible explanation of which, suggested by Cooper (1937), is that they may receive more abundant nourishment. As these hatch, the eggs originally in the interior become pushed outwards where their development is accelerated. Table 15 shows the average number, and actual total, of triungulins produced daily by five hosts each containing one fertilised female *Corioxenos*. Since it was found impossible to count accurately the number adhering externally to the host, or to remove them from the host, the figures given are not actually of the triungulins that emerged daily, but of those that left their maternal host, up to about 16h. 30 each day.

Table 16.

The length of adult life of *Antestia* containing parturient female *Corioxenos*.

		Number of instances	Total adult life (days)			Duration of life after first starting to produce triungulins		
			average	maximum	minimum	average	maximum	minimum
♂ hosts	With 1 fertilised ♀ *Corioxenos*	37	102	157	52	20	95	1
	With 2 fertilised ♀ *Corioxenos*	33	88	125	53	12	39	1
♀ hosts	With 1 fertilised ♀ *Corioxenos*	33	110	165	53	30	58	3
	With 2 fertilised ♀ *Corioxenos*	47	98	152	60	24	85	1

Table 17.

The period of development of male *Corioxenos*, from the entry of the triungulin to the emergence of the adult.

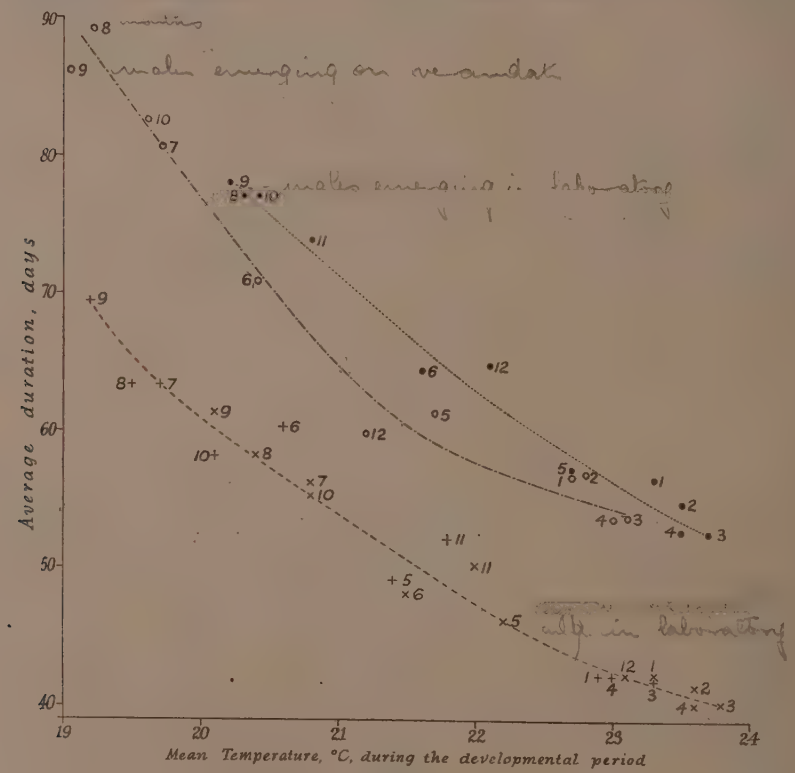
Month of emergence	In laboratory						On verandah of laboratory					
	No. of Emergences	Max. period	Min. period	Av. period	Mean temp. during av. period	Mean range of temp.	No. of emergences	Max. period	Min. period	Av. period	Mean temp. during av. period	Mean range of temp.
1935												
Nov.	45	86	66	74	20·8	2·8	—	—	—	—	—	—
Dec.	58	74	59	65	22·1	2·7	18	67	57	60	21·2	5·7
1936												
Jan.	42	59	53	57	23·3	2·5	30	62	54	57	22·7	5·9
Feb.	7	58	53	55	23·5	2·4	13	64	53	57	22·8	5·8
March	31	60	51	53	23·7	2·3	53	61	50	54	23·1	5·7
April	19	56	51	53	23·5	2·4	22	59	51	54	23·0	5·2
May	32	64	53	58	22·7	2·0	20	66	56	62	21·7	4·0
June	8	67	62	64	21·6	1·7	8	75	69	71	20·4	3·2
July	2	78	74	76	21·0	1·8	21	89	78	81	19·7	3·3
Aug.	21	86	74	77	20·3	2·0	10	93	84	89	19·2	3·3
Sep.	27	85	75	78	20·2	2·4	47	92	83	86	19·0	3·4
Oct.	34	84	73	77	20·4	2·7	28	94	75	82	19·6	3·9

Temperatures are given in ° C.

Table 16 shows the average time for which parturient hosts, kept in the laboratory, survived after first starting to produce triungulins. A fair average estimate is, therefore, that one female *Corioxenos* will produce about 50 triungulins a day for 20 days, under laboratory conditions. It is probable that in the field the duration of fecundity is somewhat longer, since many of the hosts kept in the laboratory became infected with *Penicillium* and therefore died prematurely. This fungus has been found in stylopised hosts collected in coffee plantations, but not in any large proportion of them. Moreover, when parturient hosts are kept in small containers in the laboratory it often happens that very large numbers of *Corioxenos* of the second generation start to develop in them (see also Section 3). This undoubtedly hastens the death of the host more than under natural conditions.

(7) The Influence of Temperature on the duration of the Life-cycle.

Most of the information under this head is derived from data on the developmental period of the male, and on the time elapsing between fertilisation of the female and the appearance of the triungulin larvae, under different conditions



37

Fig. 37.—The period of development of *Corioxenos* in relation to the temperature.

of temperature. These are the only two periods in the life-cycle of *Corioxenos* that can be determined with exactitude without killing the host. Table 17 shows the maximum, minimum and average period of development of 596 males, according to the month in which they emerged; the mean temperature and the mean range of temperature during the average period of development is also given. Of these males 326 emerged from hosts kept in the laboratory, where the range of temperature was small. The remaining 270 were from hosts kept on an enclosed verandah, where the mean temperature was slightly lower than in the laboratory, but the range considerably greater.

It is at once apparent that quite a small difference in temperature has a large effect on the length of the development period. Thus those emerging in the laboratory in March had taken on the average 53 days, during which period the mean temperature was 23·7°. Those emerging in September had averaged 78 days, or nearly 50% longer, though the mean temperature during those 78 days was only 3·5° lower.

These results are also shown graphically in fig. 37, from which it will be seen that, for a given mean temperature, development tended to be rather quicker on the verandah than in the laboratory. The temperature on the verandah was more variable, with higher maxima and lower minima, and this may be the cause of the slight acceleration.

I have made only a few experiments in an incubator at approximately constant temperatures, the following data being obtained. At 28·7°, 49 days (a single male only); at 26·0°, 50 days; at 25·0°, 49–50 days; at 24·5°, 50 days; at 22·8°, 57–59 days. These are rather longer periods than one would expect from an extrapolation of the curves in fig. 37, which may also be an indication that a too constant temperature has a retarding effect on development. If this is so, it does not apply to the development of the eggs, the curve for which is also shown in fig. 37.

Table 18 shows the time required for the development of the eggs, from

TABLE 18.

The incubation period of *Corioxenos*, from fertilisation until the appearance of the first triungulin larvae.

Month triungulins appeared	In laboratory			On verandah		
	No. of instances	Av. incubation period (days)	Mean temp. during incubation period (° C.)	No. of instances	Av. incubation period (days)	Mean temp. during incubation period (° C.)
1935.						
December	6	42	23·1	—	—	—
1936.						
January	7	42	23·3	5	42	22·9
February	5	41	23·6	—	—	—
March	3	40	23·8	3	42	23·3
April	13	40	23·6	10	42	23·0
May	7	46	22·2	7	49	21·4
June	7	48	21·5	1	60	20·6
July	8	56	20·8	1	63	19·7
August	2	58	20·4	1	63	19·5
September	4	61	20·1	4	69	19·2
October	13	55	20·8	2	58	20·1
November	14	50	22·0	14	52	21·8

fertilisation until the appearance of the first triungulins, during different months of the year. Since it is based on only 137 hosts containing fertilised females, of which 89 were kept in the laboratory and 48 on the verandah, the numbers for some of the months are necessarily small. However, the very great influence of comparatively slight temperature changes is clearly seen. Thus, both in the laboratory and on the verandah, the incubation period of eggs hatching during November was ten days longer than that of eggs hatching during April, yet the difference in the mean temperature during the two incubation periods was only 1·6° in the laboratory and 1·2° on the verandah.

The shortest period recorded for the development of the eggs is 34 days, in an incubator at a temperature almost constant between 24·5° and 25·0°.

Data on the developmental period of the female during the cool season are somewhat scanty, owing to there not always being a male available with which to ascertain whether a female had actually become adult or not. However, during July and August, the mean temperature being about 20·5°, no female was fertilised less than 45 days after it had, as a triungulin, entered its host. This compares with 31–34 days when the mean temperature was about 23·5°.

In general it can be deduced from the foregoing data that between the limits of about 23·5° and 19·5°, a drop of 4·0° in the mean temperature increases the life-cycle by 60%, of 3·5° by 50%, of 3·0° by 40%, of 2·5° by 33%, and of 1·5° by 15%.

(8) The Proportion of the Sexes.

Tables 19 and 20 show the number and sex of the extruded *Corioxenos* found in each one of 1000 stylopised *Antestia* collected in coffee plantations, and bred in the laboratory, respectively.

Nearly 50% of the hosts collected in the field had only one extruded parasite; the maximum number found, in fourteen hosts only, was five. The total number in the 1000 hosts was 1858. Of the parasites 42·6% were males, this proportion being virtually identical in both male and female hosts.

The sex ratio of the extruded *Corioxenos* in hosts bred in the laboratory is slightly different, for the following reasons. Many of these hosts had had more triungulins placed on them than could possibly find room to become extruded, and the total number of extruded parasites (2626) is considerably greater than that in the hosts stylopised under natural conditions. Five extruded parasites were found in 55 hosts, six in 8, and seven (the maximum number recorded) in 2.

Since it is an uncommon occurrence for more than two females to become extruded in one host (Section 6) whereas three or four males may frequently do so (I have twice recorded five and once six), it is clear that the greater the average number of parasites per host, the higher the proportion of males will be. Table 21, based on the same data, shows how the proportion of males tends to rise according to the number of parasites that become extruded.

There is some tendency, apparent both in the collected and the bred hosts, for the higher numbers of parasites, four or more, to be more frequent in female than in male hosts. This is no doubt explained by the slightly greater size of female *Antestia*. Consequently when the rate of parasitism is high there will be a slight tendency for female hosts to produce a greater proportion of male *Corioxenos*, as is evident from Table 20, but apart from this the sex of the parasite is not in any way influenced by the sex of the host.

Table 19.

The number of extruded *Corioxenos*, and the proportion of the sexes, found in 1000 stylopised *A. lineaticollis* collected in the field.

No. and sex of extruded *Corioxenos*	1 ♂	1 ♀	2 ♂	1 ♂ + 1 ♀	2 ♀	3 ♂	2 ♂ + 1 ♀	1 ♂ + 2 ♀	3 ♀	3 ♂ + 1 ♀	2 ♂ + 2 ♀	1 ♂ + 3 ♀	5 ♂	3 ♂ + 2 ♀	2 ♂ + 3 ♀	Total no. of hosts	Total no. of ♂ *Corioxenos*	= % ♂♂	Total no. of ♀ *Corioxenos*	= % ♀♀
♂ hosts	73	123	15	45	48	5	25	28	3	4	12	1	1	3	—					
% with	1 parasite 50·8		2 parasites 28·0			3 parasites 15·8				4 parasites 4·4			5 parasites 1·0			386	292	42·8	390	57·2
♀ hosts	114	167	23	63	80	10	36	63	6	4	33	5	—	9	1					
% with	1 parasite 45·8		2 parasites 27·0			3 parasites 18·7				4 parasites 6·9			5 parasites 1·6			614	500	42·5	676	57·5
Total hosts	187	290	38	108	128	15	61	91	9	8	45	6	1	12	1					
% with	1 parasite 47·7		2 parasites 27·4			3 parasites 17·6				4 parasites 5·9			5 parasites 1·4			1000	792	42·6	1066	57·4

Table 20.

The number of extruded *Corioxenos*, and the proportion of the sexes, found in 1000 stylopised *A. lineaticollis* bred in the laboratory.

No. and sex of extruded *Corioxenos*	1 ♂	1 ♀	2 ♂	1 ♂ + 1 ♀	2 ♀	3 ♂	2 ♂ + 1 ♀	1 ♂ + 2 ♀	3 ♀	4 ♂	3 ♂ + 1 ♀	2 ♂ + 2 ♀	1 ♂ + 3 ♀	4 ♂ + 1 ♀	3 ♂ + 2 ♀	2 ♂ + 3 ♀	5 ♂ + 1 ♀	4 ♂ + 2 ♀	6 ♂ + 1 ♀	5 ♂ + 2 ♀	Total no. of hosts	Total no. of ♂ *Corioxenos*	= % ♂♂	Total no. of ♀ *Corioxenos*	= % ♀♀
♂ hosts	34	63	22	63	75	14	46	68	6	1	17	54	2	3	13	1	1	3	1	—					
% with	1 parasite 19·9		2 parasites 32·9			3 parasites 27·5				4 parasites 15·2				5 parasites 3·5			6 parasites 0·8		7 parasites 0·2		487	584	47·4	647	52·6
♀ hosts	43	45	23	61	74	17	38	65	6	2	30	62	4	11	25	2	—	4	—	1					
% with	1 parasite 17·1		2 parasites 30·8			3 parasites 24·6				4 parasites 19·1				5 parasites 7·4			6 parasites 0·8		7 parasites 0·2		513	712	51·0	683	49·0
Total hosts	77	108	45	124	149	31	84	133	12	3	47	116	6	14	38	3	1	7	1	1					
% with	1 parasite 18·5		2 parasites 31·8			3 parasites 26·0				4 parasites 17·2				5 parasites 5·5			6 parasites 0·8		7 parasites 0·2		1000	1296	49·35	1330	50·65

TABLE 21.

The proportion of sexes of extruded *Corioxenos*, according to the number that developed in each host.

No. of extruded *Corioxenos* per host	No. of hosts	No. of ♂ *Corioxenos*	= % ♂♂	No. of ♀ *Corioxenos*	= % ♀♀
(*a*) Collected in the field (1000)					
1	477	187	39·2	290	60·8
2	274	184	33·6	364	66·4
3	176	258	48·8	270	51·2
4	59	120	50·9	116	49·1
5	14	43	(61·4)	27	(38·6)
(*b*) Bred in the laboratory (1000).					
1	185	77	41·6	108	58·4
2	318	214	33·6	422	66·4
3	260	394	50·5	386	49·5
4	172	391	56·8	297	43·2
5	55	176	64·0	99	36·0
6	8	33	(68·8)	15	(31·2)
7	2	13	(81·3)	3	(18·7)

PART III.

THE RELATION BETWEEN *ANTESTIA* AND *CORIOXENOS*.

(1) EXTERNAL SIGNS OF STYLOPISATION.

Certain species of Hymenoptera, when stylopised, differ in their external characters very noticeably from unstylopised specimens, so much so that Imms (1934) has stated that "much confusion has consequently arisen through the founding of new species on stylopised individuals." As a rule males tend to assume the secondary sexual characters of females and *vice versa*.

Antestia suffer no such effects when parasitised by *Corioxenos*. Except in the terminal segments of the abdomen there is no sexual dimorphism in *Antestia*. Males are, however, on the average rather smaller than females. But the larger males equal or exceed in size the smaller females.

Measurements were made of (*a*) the length of the scutellum, (*b*) the breadth of the head across the eyes, of 40 unstylopised and 40 stylopised individuals of each sex of *A. lineaticollis*. All the 160 bugs thus measured had been bred under similar conditions in the laboratory and fed on the same food—full-sized but still green coffee berries. Measurements are given in units of an eye-piece micrometer, one unit being equal to 0·0476 mm. Table 22 compares the two sexes of unstylopised bugs. The sex difference in size is clearly significant, the value for measurement (*a*) being over twelve times, and for measurement (*b*) about nine times its standard error.

Tables 23 and 24 compare the males and females respectively of stylopised and unstylopised bugs. The reduction in size of males, consequent upon

TABLE 22.

The difference in size between the sexes of unstylopised *Antestia*.

	♂♂	♀♀	Difference between means	Standard error of difference
(*a*) Mean length of scutellum	66·2	73·3	7·1	± 0·577
Variance	5·85	7·46		
Variance of the mean . .	0·146	0·187		
(*b*) Mean breadth of head .	47·5	49·9	2·4	± 0·272
Variance	1·64	1·31		
Variance of the mean . .	0·041	0·033		

TABLE 23.

The difference in size between unstylopised and stylopised males.

	Unstylopised	Stylopised	Difference between means	Standard error of difference
(*a*) Mean length of scutellum	66·2	65·0	1·2	± 0·562
Variance	5·85	6·80		
Variance of the mean . .	0·146	0·170		
(*b*) Mean breadth of head .	47·5	46·8	0·7	± 0·307
Variance	1·64	2·13		
Variance of the mean . .	0·041	0·053		

TABLE 24.

The difference in size between unstylopised and stylopised females.

	Unstylopised	Stylopised	Difference between means	Standard error of difference
(*a*) Mean length of scutellum	73·3	70·0	3·3	± 0·715
Variance	7·46	12·97		
Variance of the mean . .	0·187	0·324		
(*b*) Mean breadth of head .	49·9	48·4	1·5	± 0·345
Variance	1·31	3·435		
Variance of the mean . .	0·033	0·086		

stylopisation, is suggestive of a real effect but is not necessarily significant, since for measurement (*a*) the difference between the means is scarcely twice the standard error, and for measurement (*b*) only a little more than twice. There can, however, be no doubt that stylopisation tends to reduce the size of females, since for both measurements the difference between the means is some four times the standard error.

This small reduction in size, although of theoretical interest, is of no value in determining whether an individual is stylopised or not. Stylopisation does not affect the coloration. It is, therefore, often impossible to tell from external examination whether an *Antestia* is stylopised. It is always impossible with immature *Antestia*, in which no external signs of stylopisation can be seen. (The point of entry of the triungulin is not, after a few hours, visible even by microscopic examination.) In adult *Antestia* also, provided that stylopisation is not excessive, say not more than one male and two females in a host, it is usually impossible to detect the presence of the parasite by superficial examination. The male puparia, at least if only one or two are present, are entirely hidden under the scutellum, and the females are usually so well concealed under the wings that they are invisible even when the host is viewed from the side with a lens. Sometimes, however, particularly when two or more males are also present, a female is so much pushed out to the side that the margin of its cephalothorax is readily visible. Also when a host contains two, three, or more males, its wings may not lie in close apposition to the dorsum of the abdomen, and any contained females are then, if not conspicuous, at any rate just visible.

If a male host contains a large number of *Corioxenos*, and especially if it has one or two parturient females, its aedeagus remains permanently extended. This, however, is not a very reliable indication of stylopisation since I have seen a few unstylopised males in the same condition. Very heavily stylopised individuals are rather more sluggish and find some difficulty in flying, although one containing two male puparia and two adult (not fertilised) females was able to fly in an apparently normal manner.

(2) Internal Effects of Stylopisation.

Since the presence of *Corioxenos* shortens the life of *Antestia* only a little (Section 3), it is clear that no serious injury can be done to the internal organs. Moreover, the method by which the parasite feeds, by diffusion on the blood of the host, does not cause any structural damage. Even when an *Antestia* is stylopised at an early stage, all the organs develop in an apparently normal manner and, with the exception of the sexual organs, actually function normally. The alimentary canal may be pushed far out of its natural position, but it is unimpaired in efficiency. It may even have more work to do, since I suspect, though I have not proved, that stylopised *Antestia* feed more than unstylopised ones.

The actual effect on the sexual organs is, however, very great. With few exceptions the ovarioles of a stylopised *A. lineaticollis* (fig. 38) never produce mature eggs. Out of over 600 females bred in the laboratory, only five, each with a single *Corioxenos* that had entered at the final ecdysis, contained from five to thirteen apparently mature eggs. I also have a very few records of females collected in the field, each with only one parasite, that contained a few eggs in their ovaries. But I have never known a stylopised female *A.*

lineaticollis to oviposit, even when it had had access to an unstylopised male with which it had copulated.

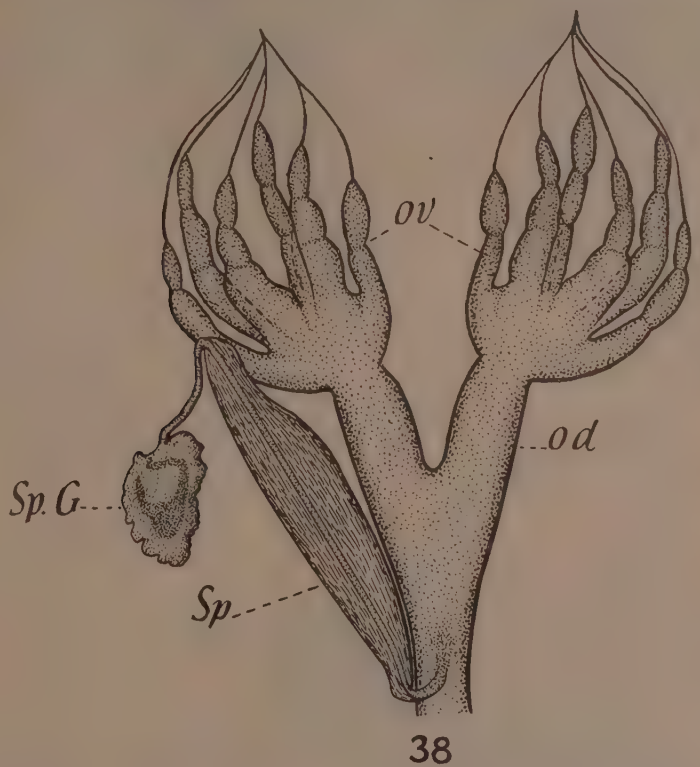


FIG. 38.—*A. lineaticollis*. Reproductive organs of female (stylopised). × 20.

Stylopised females are, therefore, invariably infertile. So also, as a rule, are stylopised males, though there are exceptions to this when the male did not become stylopised until either the fifth or adult instar. Thirty unstylopised virgin females were enclosed in one cage with twenty males which had become stylopised at the third or fourth instar. Copulation was observed on several occasions, but although about 85 egg batches were laid, no single egg hatched.

Table 25 shows the results of 20 experiments in which an unstylopised virgin female was kept separately with a stylopised male, from the time the latter became adult. (It should be mentioned that pairs of unstylopised *Antestia* kept under the same conditions have invariably produced from ten to twenty batches of fertile eggs. Most often all the eggs hatch, only seldom has more than one egg of a batch proved infertile. Unfertilised females usually lay from two to four batches, and then cease ovipositing.)

It will be seen that although several of the males that had not become stylopised until the fifth or adult instar were to some extent fertile, none of the females fertilised by them laid a normal number of viable eggs.

*

39

Fig. 39.—*A. lineaticollis.* Reproductive organs of male (unstylopised). × 19.

The reason why stylopised males should be infertile, apart from the exceptions detailed in Table 25, is obscure. I have examined the testes of a large number, including several with three or four extruded parasites which had entered at an early ecdysis; active spermatozoa, apparently indis-

tinguishable from those produced by unstylopised males, were always abundant. Moreover, stylopised males readily copulate; I have seen one do so five hours after three male *Corioxenos* had emerged from it. Careful examination has revealed no difference in either the size of the testes or in the accessory glands of stylopised males. Fig. 39 shows the genital organs of an unstylopised male *A. lineaticollis*, but the figure would do equally well for one containing several *Corioxenos*. The functions of the accessory genital glands of PENTATOMIDAE are not known, and it is possible that, although they appear to be unimpaired, their secretions are somehow affected by stylopisation.

TABLE 25.

The fertility of eggs laid by unstylopised female *Antestia* which had been paired with stylopised males.

No. and sex of the *Corioxenos* in the ♂ *Antestia*	Instar at which they entered	No. of egg batches laid by the female	No. of eggs that proved fertile
2 ♀♀	Third	3	none
2 ♂♂, 1 ♀	Fourth	3	none
1 ♂, 3 ♀♀	,,	2	none
1 ♂, 1 ♀	,,	2	none
3 ♂♂, 2 ♀♀	Fifth	2	none
3 ♂♂, 1 ♀	,,	4	none
1 ♂, 2 ♀♀	,,	2	none
1 ♂, 2 ♀♀	,,	1	none
1 ♂, 1 ♀	,,	3	none
1 ♀	,,	2	none
2 ♂♂, 1 ♀	,,	5	all of first three batches
1 ♂, 1 ♀	,,	2	all of first batch
2 ♀♀	,,	3	two eggs of first batch
1 ♀	,,	4	all of first batch
1 ♂, 1 ♀	Adult	3	none
2 ♀♀	,,	3	none
3 ♂♂	,,	4	a single egg of first batch
1 ♂	,,	7	all the first six batches
1 ♂	,,	6	all
1 ♂	,,	4	all the first three batches

(3) THE EFFECT OF STYLOPISATION ON THE DURATION OF THE STADIA AND ON THE LENGTH OF ADULT LIFE.

A comparison of the duration of the fourth and fifth stadia was made with 23 unstylopised *Antestia* and 23 that had become stylopised at the third ecdysis; all other conditions were similar. No difference was found, the aggregate number of days spent in the fourth stadium by the 23 nymphs being 311 for the unstylopised and 314 for the stylopised. In the fifth stadium it was 401 and 400 respectively.

Stylopisation does, however, tend to reduce the duration of adult life, though not so much as in some other hosts of Strepsiptera (Pierce, 1909).

Table 26 shows the average and maximum duration of adult life of 415 *Antestia*, according to the number of *Corioxenos* (including those that failed to become extruded) contained in each host. Though it is clear that excessive stylopisation does reduce longevity, yet some individual hosts containing

several parasites have survived for a period much longer than the average life of unstylopised *Antestia*.

Although many hosts of Strepsiptera die soon after the emergence of the male parasite (Perkins, 1905; Pierce, 1909) this is not so with *Corioxenos*, except perhaps when the empty puparium becomes infected with *Penicillium* (Section 6). Table 27 shows the average length of life of 350 hosts after the emergence from them of male *Corioxenos*. If the emergence of males tended to shorten the life of the host, it would be expected that there would be a close correlation between the number of males that emerged and the subsequent length of the host's life. But this is not so, except perhaps when four or five males were produced by one host.

It is, however, probable that the presence of parturient female *Corioxenos* may have some effect in hastening the death of the host, since for both sexes of the host those with two parturient females lived on the average a shorter time than those with only one (Table 16 in Part II, Section 6). The fact that the average duration of life of these stylopised *Antestia* was almost identical with that of unstylopised ones does not necessarily refute this supposition, since only those hosts which are reasonably long lived will survive long enough to produce parturient female *Corioxenos*.

It is remarkable that the presence of such a large parasite as *Corioxenos* should have such a small effect on the longevity of its host. It may be that any debility caused by stylopisation is compensated by the resulting inactivity of the sexual organs.

TABLE 26.

The average duration (in days) of adult life, according to the number of *Corioxenos* (whether extruded or not) contained in each host.

No. of *Corioxenos* per host	Male hosts			Female hosts		
	Instances	Av.	Max.	Instances	Av.	Max.
0	20	98	197	30	121	245
1–2	41	94	322	48	100	234
3–4	77	70	202	88	78	162
5–6	44	54	169	50	70	188
7–13	8	29	57	9	67	167

TABLE 27.

The average time of survival (in days) of 350 hosts after the emergence of male *Corioxenos*.

No. of ♂ *Corioxenos*	Male hosts			Female hosts		
	Instances	Av.	Max.	Instances	Av.	Max.
1	72	53	281	98	56	195
2	58	48	150	65	55	127
3	12	51	165	33	47	110
4	1	—	33	10	35	79
5	1	—	32	—	—	—

(4) Premature Mortality of Nymphal Hosts.

When breeding unstylopised *Antestia* in the laboratory, provided that they are fed on full-sized but still green berries (Part I, Section 3), there is very little mortality among nymphs, at any rate after the second ecdysis and apart from the comparatively few deaths clearly due to an imperfect and usually delayed ecdysis. Some of the few recorded deaths, not connected with an imperfect ecdysis, were probably due to injuries accidentally caused while changing the food.

When, therefore, stylopised *Antestia* have died before becoming adult, it is reasonable to assume that stylopisation has most often been the cause of death. This is, however, not a common occurrence, as is shown from the following few cases out of the many hundred stylopised nymphs that have been successfully bred to maturity in the laboratory.

(*a*) Three instances only of the contained parasite larvae, not so far developed as to extrude normally even if their host had become adult, rupturing the host's abdomen at the time of its ecdysis. *E.g.* Six triungulins penetrated a nymph at its second ecdysis on 11.xii.35; the third ecdysis took place on 23.xii and the fourth was begun on 4.i.36, but before the exuviae were completely shed some of the six larvae (which were in the fourth and fifth parasitic instars) had ruptured the abdomen of the host under the scutellum. The host died almost immediately.

(*b*) Two instances only in which death may have been due to some of the parasite larvae remaining in the thorax. In one of these a fifth-instar nymph died and was found to have two fifth-instar larvae in its thorax as well as five in its abdomen; in the other there were three fourth- and fifth-instar larvae in the thorax and four in the abdomen.

(*c*) Sometimes excessive parasitism undoubtedly causes the death of the nymph. Thus if six or more triungulins penetrate at the second ecdysis, or fifteen or more at the third, the host usually does not survive to become adult.

Experimentally, of course, when a given number of triungulins are placed on a nymph of one of the earlier instars, it would be easy to obtain numerous premature deaths from super-parasitism. Under natural conditions, judging from the numbers of larvae contained in stylopised nymphs collected in the field, premature mortality from this cause is very uncommon.

Occasionally, when a stadium of the host—usually the fifth—is unduly prolonged, the contained female parasites have arrived at maturity and (once only) a male parasite has become a pupa, while still entirely within the host's abdomen. These hosts failed to become adult. Since, however, excessive delay in moulting in itself often, though not invariably, results in the death of the nymph, it cannot be said with certainty that stylopisation has caused the death of these nymphs. Moreover, when triungulins enter at an early ecdysis of the host, the resulting larvae are able successfully to postpone extrusion for several days, waiting until their host becomes adult.

(5) The Comparative Immunity from Stylopisation of *Antestia* with Malformed Antennae.

Over 1000 *Antestia lineaticollis*, kept in separate containers and with a known number of triungulins placed on each, have been bred in the laboratory. Forty-nine of these had malformed antennae, the number of segments being less than the usual five, and often some or all of the segments short and

misshapen. Five such antennae, with a normal one for comparison, are shown in fig. 40. In many of these specimens both antennae were deformed, though not always to the same extent; in a few one antenna was almost or quite normal.

Antestia with deformed antennae do not appear to be abnormal in any other respect, except that there may be a tendency for the stadia to be prolonged. The duration of the fifth stadium of 20 such deformed *Antestia*

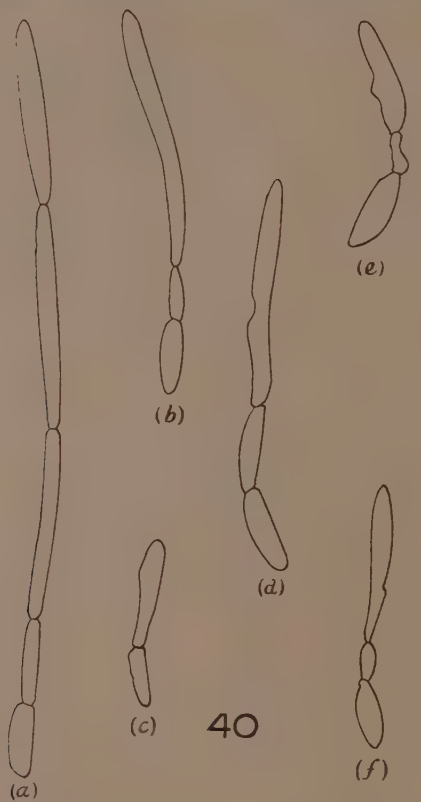


Fig. 40.—*A. lineaticollis*. Malformed antennae of individuals that failed to become stylopised. × 21.

departed from the mean of this stadium in normal individuals, at the same time and under the same conditions, by + 16 days, + 14, + 12, + 7, + 6 (2), + 3, + 2, + 1 (3), ± 0 (6), − 1, − 2 (2). The mean duration of the fifth stadium of these deformed *Antestia* was 3·2 days longer than that of the normal ones, but this is not statistically significant. The difference in variability is, however, certainly significant, the value of z being more than twice the corresponding 1 per cent. value.

This deformity is not inherited and females with imperfect antennae,

whether mated with similar or with normal males, readily pair and produce offspring normal in every way, including susceptibility to stylopisation.

However, of the 49 *Antestia* so deformed, 41 failed to become stylopised, though in one of these a single triungulin had penetrated but failed to moult. A summary of these observations is given in Table 28. The eight exceptions

TABLE 28.

Antestia with abnormal antennae, that failed to become stylopised.

Next instar of the *Antestia*	No. of instances	Total no. of triungulins placed on nymphs	Av. no. of days until next ecdysis
Adult	6	52	11
Fifth	21	145	9
Fourth	11	69	6
Third	3	15	6

TABLE 29.

Antestia with abnormal antennae, that became stylopised.

Next instar of the *Antestia*	No. of instances	Total no. of triungulins placed on nymphs	Av. no. of days until next ecdysis	No. of triungulins penetrated and developed
Adult	1	10	11	1
Fifth	3	22	8	6
Fourth	4	22	3	11

are summarised in Table 29. Of these eight, five had only one malformed antennae and two of the three which had both malformed as nymphs, when the triungulins were placed on them, had grown very nearly normal antennae by the time they were adult. Moreover, the proportion of triungulins that succeeded in penetrating and developing in these eight hosts (18 out of 54) is distinctly lower than the average for normal hosts.

Seeing that out of 1000 normal potential hosts, treated in a precisely similar way, only 57 failed to become stylopised (Table 12 in Part II, Section 3), there is clearly a correlation between malformed antennae and immunity to stylopisation. It is possible that malformation of the antennae may be, at least usually, due to a difficult ecdysis. If so, this would support the hypothesis (Part II, Section 3) that the moulting fluid, a deficiency of which might lead to a difficult ecdysis, is the stimulus that urges the triungulins to penetrate an *Antestia* that has just cast its skin.

(6) THE FUNGUS, *PENICILLIUM* SP., IN STYLOPISED *ANTESTIA*.

This fungus* is not infrequently found in hosts, bred in the laboratory, that contain an empty male puparium of *Corioxenos*. It cannot be considered an entomophagous fungus in the ordinary sense, being probably a saprophyte on *Corioxenos* and possibly a wound parasite on *Antestia*. Having gained access through a male puparium it will sometimes then attack any

* Determined by Dr. H. H. Storey, Plant Pathologist, East African Agricultura Research Station.

fertilised female in the same host; I have also twice recorded its attacking a fertilised female in a host in which no male puparium was present. In these two cases it had probably entered through the hole in the "window" of the cephalothorax, by which fertilisation had been effected. It is impossible to say whether these females were alive when attacked. I have never found it in hosts containing only un-emerged males or unfertilised females, nor in unstylopised *Antestia*.

I think that *Antestia* in which *Penicillium* has become established do not survive for long. It is difficult to be certain of this, since there are no external signs of the infection and the presence of the fungus can only be determined by dissecting the host. Most of the stylopised *Antestia* (over 1000) that have been bred in the laboratory have been examined either just after they had died or when they were clearly on the point of death. It is suggestive that it is only in these that *Penicillium* has been found, and never in the comparatively few (of which about 30 contained empty male puparia and were therefore presumably liable to infection) that have been examined after having been killed while they were still apparently healthy.

I have recorded the length of life of 350 hosts after one or more male *Corioxenos* had emerged from them (Section 3, Table 27), but unfortunately did not always note whether *Penicillium* was present or not. I think, however, that it was more often present in the hosts that died comparatively early, and this would also be an indication that it accelerates the death of the host. Should this be so, it is certain that *Penicillium* has an adverse effect on *Corioxenos*. For though it does not matter how soon a host that has produced only males should die, many hosts that have already produced males, and are therefore liable to attack by the fungus, also contain fertilised females. Premature death of such hosts will therefore result in a reduction of the number of triungulins produced.

Perkins (1905) describing an apparently similar fungus attacking *Elenchoides* (*Elenchus*), a parasite of Delphacidae, also concluded that it caused early mortality of the host. However, he was of the opinion that for this reason it was beneficial and that in any attempted introduction of *Elenchoides* the fungus should also be introduced. I am positive that the reverse is the case with the fungus attacking *Corioxenos*, though, since it is probably a species that is everywhere abundant, and since in any case fungus infection is much less usual in stylopised *Antestia* found in the field than in those bred in the laboratory, it is unlikely to be of much importance.

(7) Seasonal Variation in the Percentage of Stylopised *Antestia* in the Field.

I have made several counts, at somewhat irregular intervals between February 1935 and October 1936, of the percentage of stylopised *Antestia* collected in coffee plantations in the vicinity of Lyamungu. In these counts, which are summarised in Table 30, only adult *Antestia* were examined, and only those with extruded parasites were recorded as stylopised. The figures given for the percentage of stylopisation are therefore rather lower than they should be, but time did not permit of making, with large numbers of *Antestia*, the careful dissections necessary to detect the presence of unextruded parasites.

The fluctuations are large, from 84% stylopised in May 1935 to only 12% in December, with a rapid increase to 54% two months later.

It does not appear possible to correlate the recorded fluctuations with any weather conditions during the preceding few months, except that there may be a tendency for the rate of stylopisation to fall during the cool season. This would be expected, partly on account of the longer time required for the life-cycle and partly because the more sluggish habits of *Antestia* nymphs in cold weather may render them less likely to pick up triungulins. There seems to be no correlation whatever with rainfall. The highest rate of stylopisation (in May 1935) was after four wet months in which over 1500 mm. of rain fell, and the lowest (in December 1935) after five dry months in which the total fall was only 180 mm. Then, with the rainfall still below the average, the rate rose sharply, and it decreased again between June and August 1936, when the rains were exceptionally heavy and prolonged.

The high rate of parasitism in May 1935 can possibly be accounted for by the intensive spraying campaign (with arsenic bait spray) that had been carried out about two months previously, for I have shown (Part II, Section 3) that triungulins are able to emerge unaffected from maternal hosts that are dying of arsenic poisoning. For the rest the percentage of parasitism probably follows, with a time lag of about two months, the abundance of the host, in accordance with the law of Malthus (Muir, 1931).

TABLE 30.

Seasonal variation in the percentage of stylopised *Antestia* in the Lyamungu district.

Month collected	Male hosts			Female hosts			Total hosts		
	No. examined	No. stylopised	% stylopised	No. examined	No. stylopised	% stylopised	No. examined	No. stylopised	% stylopised
1935.									
Feb. .	270	136	50	442	225	51	712	361	51
May .	31	25	81	44	38	86	75	63	84
Sep. .	93	48	52	151	102	67	244	150	61
Dec. .	159	22	14	195	19	10	354	41	12
1936.									
Feb. .	26	17	65	35	15	43	61	32	52
June .	46	26	55	65	27	42	111	53	48
Aug. .	42	11	25	73	19	26	115	30	26
Oct. . .	38	14	37	27	8	30	65	22	34
Total of above	705	299	42	1032	453	44	1737	752	43

It will be seen from Table 30 that both sexes of the host are equally liable to be stylopised, the percentage of females attacked being very slightly, but not significantly, higher than the percentage of males.

(8) THE VALUE OF *CORIOXENOS* AS A CONTROL OF *A. LINEATICOLLIS*.

It does not appear from the literature that any species of Strepsiptera has been recorded definitely as exercising much control over the numbers of its host. Theobald (1892) believed that stylopisation was the cause of extermination of some colonies of *Andrena lapponica* Zett. at St. Leonards, England, between 1886 and 1890. But other factors may also have been at work, including, as suggested by Pierce (1909), the zealous collecting done by Theobald himself.

Muir (1906) entertained great hopes that *Elenchoides perkinsi* Pierce (*Elenchus tenuicornis* Muir *nec* Kirby), which he found in Fiji parasitising *Perkinsiella vitiensis* Kirk., would be of value in controlling the allied Hawaiian cane leaf-hopper (*P. saccharicida* Kirk.). His expectation was not, however, fulfilled, since it refused to attack the latter species.

Tillyard (1926) states that in general Strepsipterous parasites of Homoptera are to be regarded as highly beneficial.

It is difficult to evaluate the part played by *Corioxenos* in the control of *Antestia* in the coffee plantations on the slopes of Kilimanjaro, for it is clear that it is not, in the accepted meaning of the phrase, exercising an efficient control. For, in spite of the high percentage of parasitism, *Antestia* is still a serious pest which frequently causes considerable loss to the coffee crop, unless artificial control measures are taken.

But a parasite is obviously to be regarded as valuable if, as Imms (1931) has stated, its presence results in the need for less frequent artificial control measures to secure the same degree of effective control. It seems inevitable that a parasite such as *Corioxenos*, which reduces the fecundity of its host by some 40 to 50 per cent., should produce this result. It could only be otherwise if its absence meant that one or more of the egg-parasites of *Antestia* would then increase to such an extent that they would destroy a sufficiently larger percentage of the greater number of eggs that would be laid. In theory a Strepsipterous parasite should work well in conjunction with an egg-parasite. For though the Strepsipteron will reduce the number of eggs laid and therefore, by decreasing the food supply, tend to reduce the population of egg-parasites, the latter are, more than most parasites, adept at searching for their potential hosts.

Perhaps the most valuable feature of *Corioxenos* is the manner in which it fits in with the arsenic bait spray consistently advocated by Ritchie (1932), and in Tanganyika used with conspicuous success. I have proved (Part II, Section 3) that the triungulins of *Corioxenos* can emerge unaffected from *Antestia* that are dying or even dead as a result of this bait spray. It is suggestive that after application of the bait on a plantation near Lyamungu the percentage of stylopisation rose rapidly (Section 7) and the *Antestia* population remained at a low level for several months. It is still more suggestive that in Kenya, where *Corioxenos* does not occur, the arsenic bait spray does not give consistently satisfactory results (LePelley, 1932, 1934), so that reliance has to be placed on an effective, but far more expensive, method of control (LePelley, 1933).

It is known (LePelley, 1932) that the arsenic spray destroys large numbers of Hymenopterous parasites, including the egg-parasites of *Antestia*. It therefore seems very likely that this spray is only thoroughly successful where, as in Tanganyika, the work of the egg-parasites is largely replaced by that of *Corioxenos*.

Whether *Corioxenos* could be successfully introduced into another part of East Africa remains to be proved. At first sight it might be thought almost useless to introduce a parasite from one part of a continent to another, on the grounds that if it could be established in the other part it would already have become so. But the mountains of Kilimanjaro and Meru, the only localities where *Corioxenos* occurs, are virtual islands, and their fauna, in many ways different from that of the surrounding country, can have had little opportunity of becoming dispersed.

Though I am not aware of any evidence as to the original home of

Antestia, species of which are found in most tropical regions, it seems unlikely that it is Kilimanjaro. On the other hand, since *Corioxenos* has only been found on Kilimanjaro and Meru, it is probable that it is indigenous to these localities, though it may perhaps only have taken to parasitising *Antestia* in comparatively recent times. Its absence from other areas in East Africa where *Antestia* is abundant is much more likely to be due to geographical barriers having prevented its dispersal than to climatic or other factors being unsuitable.

(9) Stylopisation of Other Species of *Antestia*.

(a) *Antestia faceta* Germ.

This species has occasionally been found naturally stylopised in the Kilimanjaro district. Since, however, it is comparatively uncommon there, I have made insufficient counts to determine whether it is normally parasitised to the same extent as *A. lineaticollis*.

I have made only 38 laboratory experiments with individuals of this species kept separately, but these are sufficient to show that *Corioxenos* attacks *faceta* readily. The proportion of triungulins successful in penetrating at the third ecdysis, and then developing, seems, however, to be lower than in *lineaticollis*.

The information obtained is summarised in Table 31.

Table 31.

Stylopisation of *Antestia faceta*.

Next instar of potential host	No. of instances	No. of potential hosts that failed to become stylopised	No. of days from attachment of triungulins to next ecdysis of potential host (average)	Total no. of triungulins attached	Total no. that penetrated and developed
Adult	1	0	13	5	1
Fifth	23	2	8	119	72
Fourth	14	2	6	76	28

Owing perhaps to the smaller size of *faceta*, premature mortality due to stylopisation is of more frequent occurrence than with *lineaticollis*. However, of the 38 potential hosts with which experiments were made, 17 (9 males and 8 females) produced adult *Corioxenos* as follows :—Male hosts—1 male, 1; 1 female, 1; 2 males, 1; 1 male and 1 female, 3; 2 females, 1; 1 male and 2 females, 2. Female hosts—1 female, 3; 2 males, 1; 2 females, 2; 2 males and 1 female, 1; 3 females, 1.

It is also of interest that I have collected in the field a male *faceta* from which four male *Corioxenos* had already emerged.

Male *Corioxenos*, whether bred in *faceta* or *lineaticollis*, will readily fertilise females contained in *faceta*, though only one host survived long enough to produce triungulins, which it did over a period of 20 days before its death.

It is somewhat remarkable that the only two stylopised male *faceta* that have been put with unstylopised virgin females, proved to be potent. One

male containing one male and two female *Corioxenos*, fertilised a female which laid six batches of viable eggs. The other male contained four female parasites (two of which were not extruded) and successfully fertilised a female, which laid four batches of viable eggs. Both these males were seen to copulate within a few minutes of being put with the females. While no conclusions can be drawn from only two instances it is, considering the comparative rarity of a stylopised male of *A. lineaticollis* being potent (Section 2), at least possible that stylopisation has less effect on the male organs of *faceta*.

So far as the few records obtained show, the time required for the development of *Corioxenos*, of either sex, is the same in *faceta* as in *lineaticollis*.

The above facts indicate that *Corioxenos* would be unlikely to become established in *faceta*, where this is the only species of *Antestia* present. Where, however, *lineaticollis* and *faceta* occur together, there can be little doubt that the parasite reduces the reproduction rate of the latter species as well.

(b) *Antestia trivialis* Stål.

This species has not been recorded from the Kilimanjaro and Arusha districts and has, therefore, never been found naturally stylopised. I have found it in small numbers on arabica coffee in the East Usambaras and made the following few experiments and observations on its relations with *Corioxenos*.

Table 32 gives the results obtained from 31 nymphs kept individually in the laboratory.

TABLE 32.

Stylopisation of *Antestia trivialis*.

Next instar of potential host	No. of instances	No. of potential hosts that failed to become stylopised	No. of days from attachment of triungulins to next ecdysis of potential host (av.)	Total no. of triungulins attached	Total no. that penetrated and developed
Adult	3	2	9	Uncounted, but a very large number	11
Fifth	11	7	6	100	8
Fourth	11	9	7	87	5
Third	6	3	5	33	3

Thus of these 31 potential hosts only ten became stylopised at all, and of a total of about 300 triungulins which became attached to these potential hosts, only 27 penetrated and developed, 11 of these 27 being contained in a single host (which died prematurely). Of the remaining 16 only 7, 4 males and 3 females, arrived at maturity. The other 9 developed as far as the fifth or sixth parasitic instar but failed to become extruded and died.

Male *Corioxenos* were repeatedly introduced to the *trivialis* hosts known to contain the three extruded females, but they showed no more than a casual interest, mounting them only for a few seconds at a time and never attempting

to copulate. This is of some importance in connection with the views put forward in Part II, Section 5, concerning the sense that enables the male to find the female.

The four male *Corioxenos* that emerged from *trivialis* hosts were normal in every way, and readily copulated with females contained in *lineaticollis*.

Antestia trivialis is a larger insect than *lineaticollis* and, possibly for this reason, stylopisation seems to have less effect on the female genital organs. Three females from each of which one male *Corioxenos* had emerged, each laid a few egg batches. All the eggs were, however, infertile, although an unstylopised male had been introduced to each female and copulation had been observed. Another female, containing three female *Corioxenos* (only two extruded) was almost immediately mounted by an unstylopised male, and, though it did not oviposit, its ovaries contained fully formed eggs. Also the female in which eleven larvae developed to the fifth and sixth instars contained mature eggs in its ovaries, though none had been laid by the time of the death of the host.

The effect of stylopisation on the male organs of *trivialis* is not known, since none of the few males that became stylopised were put with unstylopised females.

It can, I think, be assumed that *trivialis* is not a normal host of *Corioxenos* and would never become naturally stylopised under field conditions. Even if, in a mixed population of *lineaticollis* and *trivialis*, a few of the latter were to be parasitised, the controlling influence of such casual parasitism could not be of any importance.

(c) *Antestia falsa* Schout.

I have only found this species in the South Paré mountains where, although *A. lineaticollis* is also abundant, *Corioxenos* does not occur. The following few laboratory experiments were made. In 20 nymphs of various instars, on which a total of 200 triungulins were placed, no *Corioxenos* larvae developed; although in three of them a few triungulins had penetrated but had failed to moult. These 20 nymphs all became adult and lived for a normal time. In 4 nymphs a total of 19 out of 45 triungulins penetrated and developed to the first or second parasitic instar, but their hosts died prematurely. One fifth-instar nymph on which 5 triungulins had been placed lived for a month after becoming adult; on its death it was found to contain a single third parasitic instar larva which had clearly died some time previous to the death of the host.

Thus of 250 triungulins placed on nymphs of this species only 20 developed at all, and only a single one as far as the third parasitic instar. It is therefore clear that *falsa* is not a normal host of *Corioxenos*. The reason is not known, for in size and general appearance *falsa* resembles *lineaticollis* more closely than *faceta* does.

No experiments have been made with *Antestia usambarica* Schout., of which I have so far only found a single female which failed to lay eggs.

Triungulins have been put on to nymphs of a number of other species of PENTATOMIDAE, but they never penetrated.

It can therefore be concluded that *Corioxenos antestiae* is a specific parasite of the genus *Antestia*, and under field conditions probably confined to the species *lineaticollis* and *faceta*.

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